Fishery Bulletin

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Seattle, Washington

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NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

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POLLUTION-ASSOCIATED DISEASES AND ABNORMALITIES OF FISH AND SHELLFISH: A REVIEW

CARL J. SINDERMANN[1]

ABSTRACT

The relationship of disease and environmental stress is becoming increasingly well established with time. Human activities—particularly those that result in chemical additions to the coastal/estuarine environment—have increased the potential stresses on fish and shellfish inhabiting those areas. Circumstantial evidence for associations of pollutants with certain fish and shellfish diseases and abnormalities is accumulating.

This paper attempts to review and evaluate existing information about associations of diseases and marine environmental degradation. Emphasis has been placed on: diseases caused by contaminant stress and related facultative pathogens; stress-provoked latent infections; environmentally induced abnormalities; genetic abnormalities associated with mutagenic and other properties of contaminants; experimentally induced lesions; contaminant effects on resistance and immune responses; and pollutant-parasite interactions.

There are several diseases, particularly fin erosion and ulcers in fish and shell disease in crustaceans, for which a relationship with pollution seems evident, and there are a number of other diseases or abnormalities (such as certain neoplasms and skeletal anomalies) for which a relationship with pollution is indicated. Furthermore, there is some evidence that certain latent viral infections may be provoked into patency by environmental stress.

Disease is a constant concomitant of life for any species, normally removing individuals from the population continuously. Marine animals are, of course, subject to a wide spectrum of diseases of infectious or noninfectious etiology ("disease" can be defined in the broad sense as "any departure from normal structure or function of an animal" or as "the end result of interaction between a noxious stimulus and a biological system").

Disfunction and death due to the activity of infectious agents constitute the narrower, but often predominant concept of disease. *Infectious diseases*—caused by viruses, bacteria, fungi, protozoa, and other pathogenic organisms—are usually prime suspects in searches for causes of mortalities, often to the exclusion of other possible causes. *Noninfectious diseases* include such phenomena as environmentally induced skeletal anomalies, genetic abnormalities, physiological malfunctions caused by chemical environmental factors, metabolic disorders resulting from nutritional deficiencies, many forms of neoplasia, and a host of others (Sparks 1972). In many instances, it is probably the combination of an infectious agent and environmental stress that eventually causes mortality.

The distinction between "infection" and "disease" must be kept in mind. Most organisms are constantly hosts to potentially pathogenic microorganisms, but disease results from imbalance of the interactive system which includes virulence of the pathogen, resistance of the host, and effects of environmental stresses.

Infectious disease usually exists in an enzootic form, weakening or disabling individuals and rendering them more susceptible to predators or other environmental stresses. Occasionally, though, epizootics and mortalities comparable to the great plagues of the Middle Ages may sweep through animal populations. In marine species we have seen such massive epizootics result in the great herring mortalities of the mid-1950's in the Gulf of Saint Lawrence (Sindermann 1958), and the extensive oyster mortalities of the 1960's in the Middle Atlantic states (Sindermann 1968). These epizootics are triggered by a complex interplay of pathogen, environment, and host population. Considering only the environmental aspects of such outbreaks, any departure from normal conditions produces a degree of stress on the population, and may contribute to an increase in prevalence of a pathogen, or of facultative invad-

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ers. Some of these environmental factors are drastic changes in temperature, lack of adequate food, or overcrowding. Resistance of the host animal to the disease is, of course, intimately related to these stresses (Snieszko 1974).

Environmental stresses have been implicated in a number of fish and shellfish diseases, but are difficult to quantify. Even a definition of stress can be elusive. Selye (1950, 1952) defined stress as the sum of all the physiological responses by which an animal tries to maintain or reestablish a normal metabolism in the face of a physical or chemical force. Brett (1958) defined it as "A state produced by any environmental or other factor which extends the adaptive responses of an animal beyond the normal range, or which disturbs the normal functioning to such an extent that, in either case, the chances of survival are significantly reduced." Another definition which identifies stress as the product and not the cause of homeostatic change is that of Esch et al. (1975): "Stress is the effect of any force which tends to extend any homeostatic or stabilizing process beyond its normal limit, at any level of biological organization."

Human activity has introduced or has increased environmental stresses for fish in estuarine and coastal waters. We have, for instance, added pesticides and other synthetic chemicals which can, even in low concentrations, drastically affect the physiology of fish and shellfish, and with which the species may have had no previous evolutionary experience. We have added heavy organic loads, in the form of sewage sludge and effluents, which can produce anaerobic or low-oxygen environments and which are often accompanied by other contaminants such as heavy metals, that can interfere with enzymes of the fish and the food organisms they consume.

During the past decade, several diseases and abnormalities of fish and shellfish have been described that seem associated with pollutant stresses. These can be categorized and discussed as:

1. Diseases caused by contaminant stress and related pathogens;
2. Stress-provoked latent infections;
3. Environmentally induced abnormalities;
4. Genetic abnormalities associated with mutagenic and other properties of contaminants;
5. Experimentally induced lesions;
6. Contaminant effects on resistance and immune response; and
7. Pollutant-parasite interactions.

In the first and second categories a synergistic activity of chemical contaminants (or other form of pollutant stress) and an infectious agent seems to be a plausible explanation for at least some of the observed effects. In categories three and four, it is sometimes difficult to determine conclusively whether environmental contaminants act directly on target tissues or biochemical pathways, or if the genetic material is first affected, with subsequent changes in structure and/or function.

During the past several years there have been signs of increasing interest in relationships between marine fish and shellfish diseases and environmental pollution. Several conferences have been held recently, including the 1974 Symposium on Tumors in Aquatic Animals, held in Cork, Ireland; the 1975 Symposium on Sublethal Effects of Pollution on Aquatic Organisms, held as part of the 13th Pacific Science Congress in Vancouver, B.C.; and the 1976 Conference on Aquatic Pollutants and Biological Effects with Emphasis on Neoplasia, held in New York. The amount of relevant literature available for consideration within the title "pollution-associated diseases and abnormalities of fish and shellfish" is somewhat overwhelming. Even the list of books containing pertinent material is impressive (Dawe and Harshbarger 1969; Snieszko 1970; Ruivo 1972; Vernberg and Vernberg 1974; Koeman and Strik 1975; Ribelin and Migaki 1975; Dawe et al. 1976; Lockwood 1976; Kraybill et al. 1977; Vernberg et al. 1977). Additionally, significant recent reviews have appeared, for example, Rosenthal and Alderdice (1976) and McIntyre[2].

This paper attempts to summarize the present state of knowledge about possible associations of fish and shellfish diseases (infectious and noninfectious) with estuarine and coastal pollution. Much of the evidence for such associations is still circumstantial and is presented as such. The original literature on this subject, as for any pollution-related subject, is voluminous. The references cited here constitute only a small but, I hope, a representative fraction of the published information available. It should also be pointed out here that this paper does not consider

[2]McIntyre, A. D. (Convenor). 1976. ICES working group on pollution baseline and monitoring studies in the Oslo Commission and ICNAF areas. Report of the subgroup on the feasibility of effects monitoring. Int. Counc. Explor. Sea, Doc. CM1976/E:44, 36 p.

physiological and behavioral disorders, which might be included in a broad definition of disease.

Finally, in these introductory comments, it should be noted that to make any firm association of a disease with environmental pollution there are several basic requirements: 1) knowledge of the history of occurrence of the disease in a particular species in the geographic area of concern; 2) knowledge of the history of occurrence and levels of particular pollutants in that area; 3) a review of the biology, life history, and occurrence of the disease in other areas, in other species, and under different environmental conditions; 4) an intensive baseline survey of the current disease and pollution situation, with attention to statistical reliability of sampling; 5) laboratory and field experimentation with the principal objective of reproducing the disease by exposure to known levels of contaminants; and 6) resurveys of the disease and pollution levels over several years, looking for changes or trends. As will become apparent in this paper, these requirements have been fully satisfied for few if any of the diseases discussed.

DISEASES CAUSED BY CONTAMINANT STRESS AND RELATED FACULTATIVE PATHOGENS

Fin Erosion

Probably the best known but least understood disease of fish from polluted waters is a nonspecific condition known as "fin rot" or "fin erosion" (Figures 1, 2), a syndrome which seems rather clearly associated with degraded estuarine or coastal environments. Fin rot has been reported from the New York Bight (Mahoney et al. 1973; Ziskowski and Murchelano 1975; Murchelano 1975), California (Young 1964; Southern California Coastal Water Research Project[3]; Mearns and Sherwood 1974), Puget Sound (Wellings et al. 1976), Biscayne Bay and Escambia Bay in Florida (Couch 1974a; Sindermann et al. 1978), the Gulf of Mexico (Overstreet and Howse 1977), the Irish Sea (Perkins et al. 1972), and the Japanese coast (Nakai et al. 1973).

Fin rot seems to occur in at least two types: one in bottom fish, where damage to fins seems site-specific and related to direct contact with contaminated sediments, and another in pelagic nearshore species, characterized by more generalized erosion, but with predominant involvement of the caudal fin.

Recent quantitative surveys along the Middle Atlantic coast have disclosed high prevalence (up to 38%) of fin rot in samples of trawled marine fishes from the New York Bight. Thus far, 22 affected species have been found. While bacteria of the genera *Vibrio*, *Aeromonas*, and *Pseudomonas* were frequently isolated from abnormal fish, a definite bacterial etiology has not been established. Fin rot disease was significantly more abundant in the New York Bight Apex, the area of greatest environmental damage, than in any comparable coastal area from Block Island, R.I., to Cape Hatteras, N.C. (Murchelano and Ziskowski 1976). An association between high fin rot prevalence and high coliform counts in sediments is emerging (Mahoney et al. 1973), as is an association between high fin rot prevalences and high heavy metal levels in sediments (Carmody et al. 1973). The disease signs can be produced experimentally by exposure of fish to polluted sediments. Fin erosion has also been observed in striped bass, *Morone saxatilis*, overwintering in heated effluents of power plants in the Middle Atlantic States.

The histopathology of fin erosion in winter flounder, *Pseudopleuronectes americanus*, from the New York Bight was examined by Murchelano (1975). Significant descriptive findings were epidermal hyperplasia accompanied by dermal fibrosis, hyperemia, and hemorrhage. Bacterial infections were not found, nor was pronounced inflammatory response. However, reference was made to acute fin lesions seen in summer flounder, *Paralichthys dentatus*, in which bacteria were readily demonstrable. The absence of pronounced inflammatory response in either species of flounder led Murchelano to suggest that the necrotic process is not primarily microbial and that activities of a chemical irritant may be involved.

Another histopathological and bacteriological study of fin rot in winter flounder from Narragansett Bay, R.I., by Levin et al. (1972) described acute ulcerative lesions as well as fin erosion, thought to be produced by *Vibrio anguillarum*. Acute inflammatory response was observed, and ulcerations were reproduced in fish exposed experimentally to *V. anguillarum* isolates. It is possible that several poorly defined disease entities or

[3]Southern California Coastal Water Research Project. 1973. The ecology of the Southern California Bight: Implications for water quality management. Ref. No. SCCWRP TR 104, El Segundo, Calif.

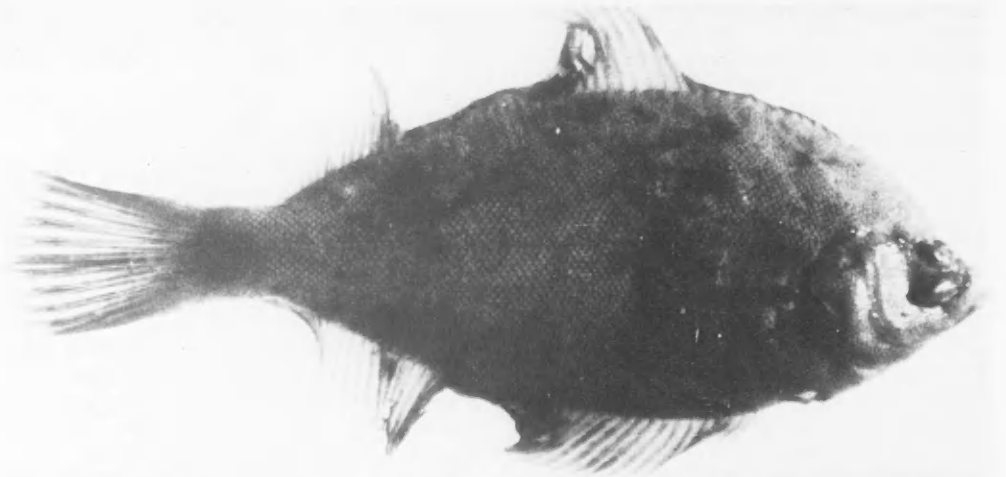

FIGURE 1.—Site-specific fin erosion concentrated in the midportion of fins in winter flounder (anterior dorsal fin is folded over in this picture). Note melanism in areas of erosion. (Photograph courtesy of J. O'Reilly, Northeast Fisheries Center Sandy Hook Laboratory, NMFS, NOAA, Highlands, N.J.)

generalized disease signs (one of which is fin erosion) may be responsible for the disparate nature of histopathological findings in this report, as compared with those of Murchelano (1975).

Fin rot, with associated mortalities, was reported by Couch and Nimmo (1974b) in Atlantic croaker, *Micropogon undulatus*, and spot, *Leiostomus xanthurus*, from Escambia Bay, Fla. The disease syndrome and mortalities were observed for several years during periods of high temperature and low dissolved oxygen. Escambia Bay has been polluted by the PCB (polychlorinated biphenyl), Aroclor[4] 1254, for a number of years (Duke et al. 1970).

Information from southern California (Southern California Coastal Water Research Project, see footnote 3) also indicates an association of fin rot with degraded habitats; relevant statements are: "The incidence of fin erosion was high in areas with high concentrations of waste water constituents in the sediments . . . ." "Although there is a definite association between fin erosion and waste water discharges, the causal factors are unknown." "Nearly half of the 72 species caught off the Palos Verdes Peninsula were affected with this syndrome" (eroded fins). It is interesting that a histopathological study of fin erosion in Dover sole, *Microstomus pacificus*, from the California coast (Mearns and Sherwood 1974; Klontz and Bendele[5]) produced findings similar to those of Murchelano (1975)—hyperplasia, fibrosis, absence of inflammation, and absence of microbial infection.

Some species either seem more resistant to fin erosion or are exposed differentially to toxic substances in water or sediments. A recent study by Wellings et al. (1976) in a heavily polluted arm of Puget Sound (the Duwamish River) in which over 6,000 fish of 29 species were examined, disclosed fin erosion only in starry flounder, *Platichthys stellatus*, and English sole, *Parophrys vetulus*. Average incidences were 8 and 0.5% respectively. Histopathological findings were similar to those for east coast and California flatfishes—epidermal hyperplasia, fibrosis, resorption of fin rays, aggregation of melanophores, mucus cell changes, and absence of bacterial invasion. The authors described briefly what may be highly relevant observations of liver pathology in starry flounder from the area where fin erosion was common. Histopathology included increased fat deposition in hepatic cells, fibrosis, and vascular distension.

Recent Japanese publications have mentioned fin erosion in fish from polluted bays. Nakai et al.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5]Klontz, G. W., and R. A. Bendele. 1973. Histopathological analysis of fin erosion in southern California marine fishes. Southern Calif. Coastal Water Res. Proj., El Segundo, Calif., Rep. TM203, 8 p.

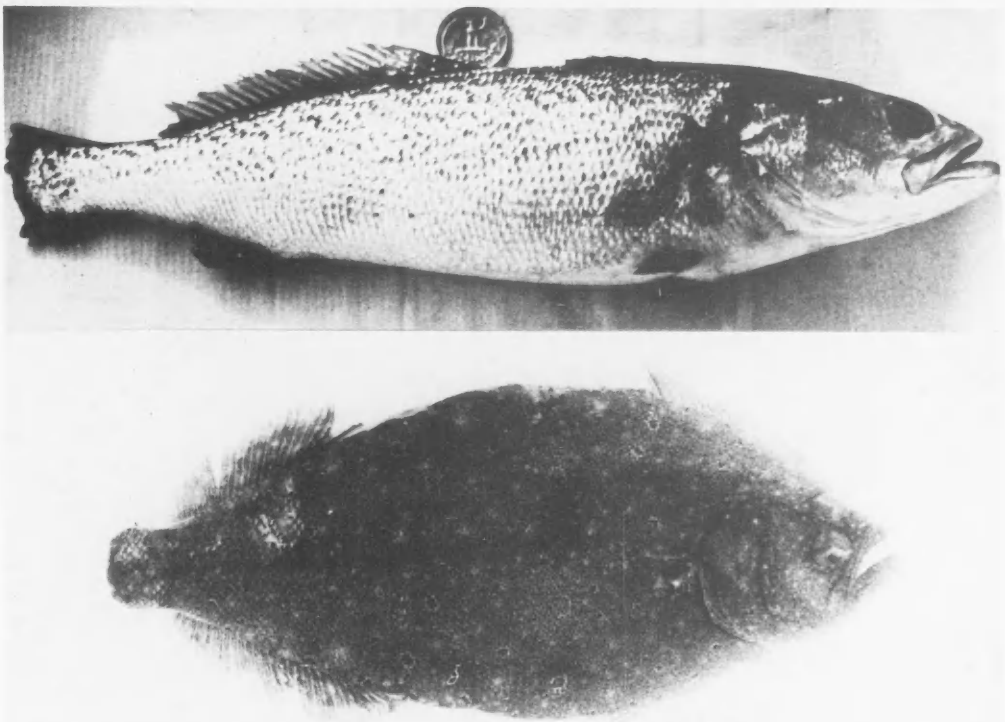

FIGURE 2.—Generalized fin erosion in weakfish, *Cynoscion regalis*, (above) and in summer flounder (below). Note that in the weakfish the anal, caudal, and pelvic fins are eroded, while the dorsal fins are not usually damaged. In contrast the summer flounder shows erosion of wide areas of the fin fringes.

(1973) found that as many as 60% of all stargazer, *Uranoscopus japonicus*, sampled from Suruga Bay had evidence of disintegration of caudal and pectoral fins. Six other species also had abnormal fins.

An increase in occurrence of fin erosion and other epidermal lesions (ulcers and lymphocystis) in flatfish from the Irish Sea since 1970 was reported by Perkins et al. (1972). Fin damage, unknown before 1970, was observed in plaice, *Pleuronectes platessa*, and dab, *Limanda limanda*, taking the form of erosion or total loss of caudal and lateral fins. Ulcers were described that "did not have the typical appearance of bacterial ulcers . . . ." The authors pointed to ocean dumping of toxic wastes, particularly of PCB's, as a possible factor contributing to observed prevalences of epidermal lesions, but no clear relationship was demonstrated. Another study conducted in the Irish Sea in 1972 (Shelton and Wilson 1973) did not identify fin erosion in plaice or dab, but did find a low incidence of "healed fin damage (probably caused by previous capture and rejection or by passage through the cod-end mesh)."

The possible role of environmental chemical contamination in the etiology of fin erosion emerges more clearly as additional studies are reported. Fish from the New York Bight, reported in studies by Mahoney et al. (1973), Murchelano (1975), and Ziskowski and Murchelano (1975), exist in a highly contaminated area, with chemicals such as heavy metals and petroleum residues in sediments far above background levels. In California, McDermott and Sherwood[6] fount DDT to be significantly higher in fish with fin erosion, and PCB levels slightly higher in such fish than in normal individuals. Both contaminants were significantly higher in Palos Verdes fish than in fish

[6]McDermott, D. J., and J. Sherwood. 1975. Annual report. Dep. Fish. Mar. Fish. Program, Coastal Water Res. Proj., El Segundo, Calif., p. 37.

from a distant control area (Dana Point). Wellings et al. (1976) found abnormally high concentrations of PCB's in English sole and starry flounders from the Duwamish River in Washington.

Several authors have postulated that fin erosion in flatfish may be initiated by direct contact of tissues with contaminated sediments. Mearns and Sherwood (1974) and Sherwood and Mearns (1977), for example, suggested that toxic substances (sulfides, heavy metals, chlorinated hydrocarbons, etc.) could remove or modify the protective mucus coat and expose epithelial tissues to the chemicals. Sherwood and Bendele[7] reported that Dover sole from the California coast with severe fin erosion produced much less mucus than normal fish.

It seems quite likely that the "fin erosion" syndrome in fish includes chemical stress, possibly acting on mucus and/or epithelium; stress resulting from marginal dissolved oxygen concentrations, possibly enhanced by a sulfide-rich environment; and secondary bacterial invasion in at least some instances. Some recent experimental information tends to support this hypothesis.

A series of experiments at the Gulf Breeze (Fla.) Environmental Research Laboratory of the U.S. Environmental Protection Agency, using the spot, resulted in experimental production of fin rot disease following exposure to 3-5 μg/l of Aroclor 1254 (Couch 1974a). Mortalities of up to 80% were reported.

Minchew and Yarbrough (1977) exposed *Mugil cephalus* in brackish water ponds (12‰) to 4-5 ppm crude oil and found that fin erosion developed in most of the exposed fish within 6-8 days. Lesions were often hemorrhagic, and a tentative *Vibrio* sp. was isolated consistently from surfaces of diseased fish, but was rarely found systemically. Fin regeneration characterized most experimental fish 2 mo after exposure. This experiment should be repeated and extended.

Experimental induction of fin erosion has followed exposure to several other contaminant chemicals. Chronic exposure of fingerling rainbow trout, *Salmo gairdneri*, to lead caused a variety of grossly visible abnormalities, including fin erosion (Davies and Everhart[8]); and chronic exposure of minnows (*Phoxinus phoxinus*) to zinc and cadmium resulted in similar abnormalities (Bengtsson 1974, 1975).

A recent report by Overstreet and Howse (1977) pointed to fin erosion and other abnormalities as indicators of gradually increasing pollution stress on the Mississippi gulf coast. Among other disease conditions noted by Overstreet and Howse was "red sore," characterized by hemorrhagic lesions beneath scales, occasional hyperplasia, and accompanying ciliate (*Epistylis* sp.) infestation of the body surfaces. The authors indicated that red sores now occur in many of the fish in some freshwater and low salinity areas of the gulf coast of Mississippi, a striking similarity to recent observations in Biscayne Bay, Fla., where many fish of many species now exhibit hemorrhagic lesions beneath the scales, a condition which was unknown a decade ago (Sindermann 1976). Red sores and associated mortalities have also been described by Rogers (1970, 1972) and Esch et al. (1976) from centrarchid fishes in freshwater reservoirs of the southeastern United States. The disease condition in freshwater seems clearly related to *Epistylis* infestation, probably abetted by secondary bacterial infections, particularly by *Aeromonas*, although there is still some question about which organism is the primary invader.

It seems likely that generalized disease signs, such as fin rot and red sores (and probably other epidermal lesions such as ulcerations, papillomas, and lymphocystis), may be characteristic of fishes resident in degraded habitats, where environmental stresses of toxic chemicals, low dissolved oxygen, and high microbial populations exist. The extent and nature of these external manifestations are probably variable with resistance of the particular species and the extent and nature of environmental degradation.

Ulcers

Next to fin erosion, probably the commonest abnormality reported from fish taken in polluted waters can be identified as "ulceration of bacterial etiology," even though precise bacterial etiology has not been demonstrated in every case. Where bacterial isolations have been made from ulcerated tissue, *Vibrio anguillarum* has been by far the most predominant organism, with pseudomonads and aeromonads in lesser abundance.

[7]Sherwood, M. J., and R. A. Bendele. 1975. Mucous production in Dover sole. Annu. rep., Coastal Water Res. Proj., El Segundo, Calif., p. 51.

[8]Davies, P. H., and J. H. Everhart. 1973. Effects of chemical variations in aquatic environments. III. Lead toxicity to rainbow trout and testing application factor concept. EPA-R3-73-011C, 80 p.

The report on ulcerations and fin rot in winter flounders from Narragansett Bay, by Levin et al. (1972) has been mentioned in the previous section. The acute ulcerative lesions were thought to be caused by *V. anguillarum* infections, and the ulcerative phase was reproduced in fish exposed experimentally to cultured *V. anguillarum* isolates.

A more recent report by Robohm and Brown (1977) described systemic bacterial infections and ulcerative lesions of the tail and dorsal muscles in summer flounder from Connecticut waters. A highly pathogenic *Vibrio* sp. was isolated, and experimental infections were produced by subcutaneous inoculation and by seeding holding tanks with bacteria at levels of 360/ml. Ulcers at the inoculation site and subcutaneous hemorrhages along the bases of fins characterized experimental infections (Figure 3). These observations resemble those of Levin et al. (1972) in winter flounder.

Ulcerations, probably of bacterial etiology, have been reported in fish of several species from the Irish Sea. Perkins et al. (1972) and Shelton and Wilson (1973) reported ulcers from European flounders (*Platichthys flesus*), dab, and plaice. Prevalences were low (1-4%) in most instances.

An "ulcer syndrome" in cod, *Gadus morhua*, from Danish coastal waters has been studied for several years and seems associated with localized areas of severe pollution (Jensen and Larsen 1976, 1977; Larsen and Jensen 1977a, b). *Vibrio anguillarum* and an *Aeromonas* species have been implicated (Sørensen 1977).

Ulcerations or external lesions on fish may, of course, have a number of causes other than bacterial infection. They may be due to net damage or other surface abrasions, or to predator attacks. Some protozoa (Myxosporida and Microsporida) can infect muscle or skin tissue and multiply to produce gross cysts. These infections mature to produce many characteristic microscopic spores, and in the process the overlying epidermis may be sloughed, producing ulcers with usually smooth borders (Figure 4). However, it seems to be a

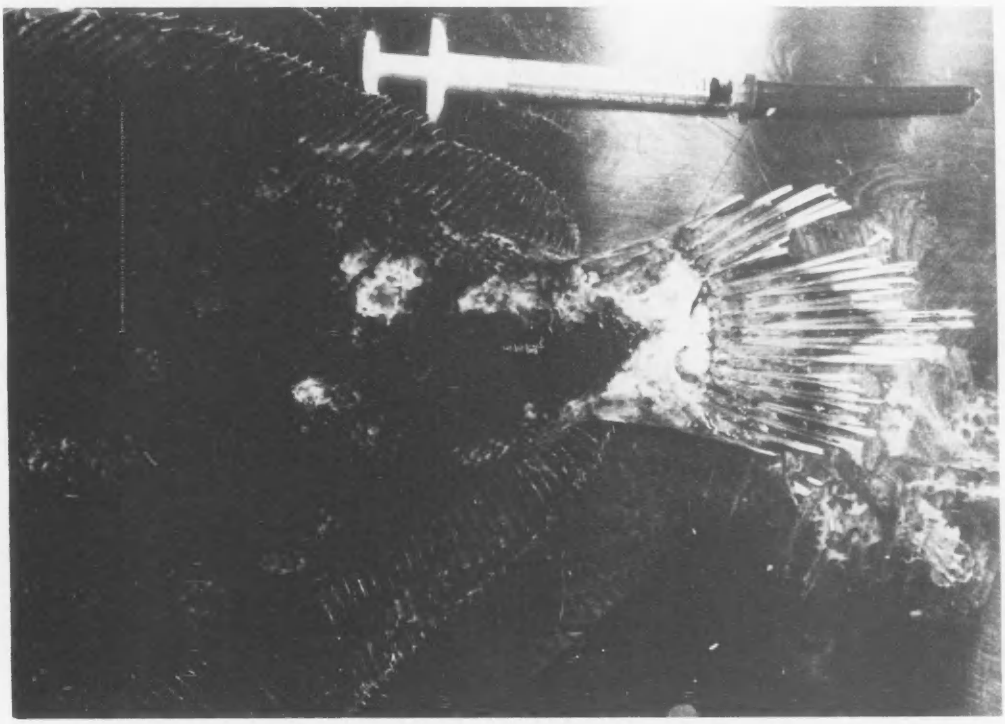

FIGURE 3.—Ulcers and fin erosion in summer flounder produced by experimental inoculation of *Vibrio* sp. (Photograph courtesy of R. Robohm, Northeast Fisheries Center Milford Laboratory, NMFS, NOAA, Milford, Conn.)

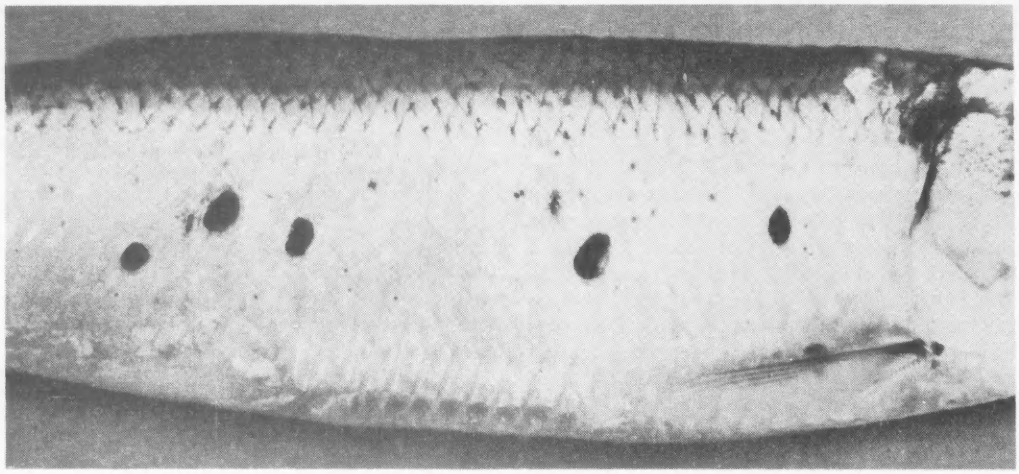

FIGURE 4.—Ulcer with smooth margins in Atlantic herring, resulting from infection by the myxosporidan protozoan, *Kudoa clupeidae*.

reasonable generalization that many of the infections that produce grossly visible ulcerations in fish are bacterial, and are often due to pathogens of the genera *Vibrio*, *Pseudomonas*, or *Aeromonas* (Lamolet et al. 1976). Ulceration often begins with scale loss or formation of small papules, followed by sloughing of the skin, exposing the underlying muscles, which may also be destroyed. Bacterial ulcers may have rough or raised irregular margins, and will often be hemorrhagic. Ulcers may or may not be associated with fin erosion.

Shell Disease of Crustacea

Also associated with badly degraded estuarine and coastal waters is a disease condition in Crustacea commonly referred to as "shell disease" or "exoskeletal disease" or "shell erosion." This can be considered in some ways as the invertebrate counterpart of fin erosion.

Homarus americanus and rock crabs (*Cancer irroratus*) from grossly polluted areas of the New York Bight were found to be abnormal, with appendage and gill erosion a most common sign, by Young and Pearce (1975). Skeletal erosion occurred principally on the tips of the walking legs, ventral sides of chelipeds, exoskeletal spines, gill lamellae, and around areas of exoskeletal articulation where contaminated sediments could accumulate. Gills of crabs and lobsters sampled at the dump sites were usually clogged with detritus, possessed a dark brown coating, contained localized thickenings, and displayed areas of erosion and necrosis. Similar disease signs were produced experimentally in animals held for 6 wk in aquaria containing sediments from sewage sludge or dredge spoil disposal sites. Initial discrete areas of erosion became confluent, covering large areas of the exoskeleton, and often parts of appendages were lost. The chitinous covering of the gill filaments was also eroded, and often the underlying tissues became necrotic.

Dead and moribund crabs and lobsters have been reported on several occasions by divers in the New York Bight Apex, and dissolved oxygen concentrations near the bottom during the summer often approach zero (Pearce 1972; Young 1973). Low oxygen stress, when combined with gill fouling, erosion, and necrosis, could readily lead to mortality.

In a related study, Gopalan and Young (1975) examined "shell disease" in the caridean shrimp, *Crangon septemspinosa*, an estuarine and coastal food chain organism common on the east coast of North America and important in the diets of bluefish, weakfish, flounders, sea bass, and other economic species. Examinations of samples of *Crangon* from the New York Bight disclosed high prevalences (up to 15%) of eroded appendages and blackened erosions of the exoskeleton. The disease condition was only rarely observed at other collecting sites (Beaufort, N.C., and Woods Hole, Mass.). Histological examination of diseased specimens produced findings similar to those of

Young and Pearce (1975) with crabs and lobsters. All layers of the exoskeleton were eroded; affected portions were brittle and easily fragmented; cracking and pitting of calcified layers occurred; and underlying tissues were often necrotic. Laboratory experiments using seawater from the highly polluted inner New York Bight resulted in appearance of the disease in 50% of individuals. Erosion was progressive, crippled individuals were cannibalized, and eroded segments of appendages did not regenerate after ecdysis. No disease signs developed in control animals held in artificial seawater.

A German study of the effects of industrial wastes on the brown shrimp, *Crangon crangon* (Schlotfeldt 1972), disclosed high prevalence of so-called "black spot disease," with signs very similar to those seen in *C. septemspinosa* from the New York Bight. Juvenile and adult shrimps from the Föhr Estuary had black areas of erosion on the carapace and appendages, with necrosis of underlying tissues, and, frequently, missing terminal segments of appendages. The disease condition varied in prevalence seasonally, with a peak of 8.9% in summer. Lesions persisted and worsened after ecdysis, and experimental exposure to detergent accelerated the course of the disease.

Shell disease of Crustacea has been observed in many species and under many conditions, both natural and artificial (Rosen 1970; Sindermann 1970). Actual shell erosion seems to involve activity of chitinoclastic bacteria, with subsequent secondary infection of underlying tissue by facultative pathogens. Initial preparation of the exoskeletal substrate by mechanical, chemical, or microbial action probably is significant; thus high bacterial populations and the presence of contaminant chemicals in polluted environments, as well as extensive detrital and epibiotic fouling of gills, could combine to make shell disease a common phenomenon and a significant mortality factor in crustaceans inhabiting degraded environments.

There is much room for study in this cloudy territory at the boundary between infectious and noninfectious disese processes, as exemplified by fin and shell erosion. This is the area where environmental stress and facultative microorganisms exert their impacts; where high bacterial populations in eutrophic waters interact with exposed, or injured, or chemically modified surface membranes; where epibiotic fouling organisms can assume pathogenic roles; and where nonspecific lesions such as fin rot and skeletal erosions can occur in epizootic proportions.

Lymphocystis

While fin erosion, ulcers, and shell disease seem to have reasonable associations with degraded environments, it is difficult to find additional good examples in the category of "Diseases caused by facultative pathogens." Probably the most likely candidate (in an obviously poor field) would be lymphocystis, a virus disease which causes extreme hypertrophy of fibroblast cells in a large number of freshwater and marine fishes, and which has been postulated to be associated with environmental stresses. Perkins et al. (1972) found in a 1971 survey that three diseases—lymphocystis, epidermal ulcers, and fin erosion—were abundant in plaice and dab from the Northeast Irish Sea. Lymphocystis infection levels in individual trawl catches ranged from 0 to 25% in plaice and from 0 to 17% in dab. The authors pointed out that the Irish Sea has been used recently for dumping of toxic wastes, particularly PCB's, but their concluding statement is ". . . there is insufficient evidence to be certain whether the increased incidence of the diseases noted in 1971 is the result of an outbreak of epidemics of purely biological origin or if the dumping of toxic wastes is responsible."

Another survey of lymphocystis in the Irish Sea, this one in 1972, was reported by Shelton and Wilson (1973). They found lymphocystis to be the most abundant of observable pathological conditions, with highest prevalence (14.6%) in flounder, *Platichthys flesus*, and lesser prevalences in other flatfish (1.9% in plaice and 1.1% in dab). Unlike Perkins et al. (1972), Shelton and Wilson considered recent pollution of the Northeast Irish Sea to be the least likely explanation for high levels of lymphocystis—pointing out that the disease has been known from that area for 70 yr, having been described early in the century by Woodcock (1904) and Johnstone (1905) from flounders taken in the Irish Sea. Van Banning (1971) studied lymphocystis in North Sea plaice (Figure 5) and also concluded that pollution was not a likely cause of high prevalences.

A recent lymphocystis epizootic with over 50% prevalence was reported from flatfish in the North Sea by Mann (1970) and earlier epizootics have occurred in Europe (Weissenberg 1965). Templeman (1965) reported an epizootic in American

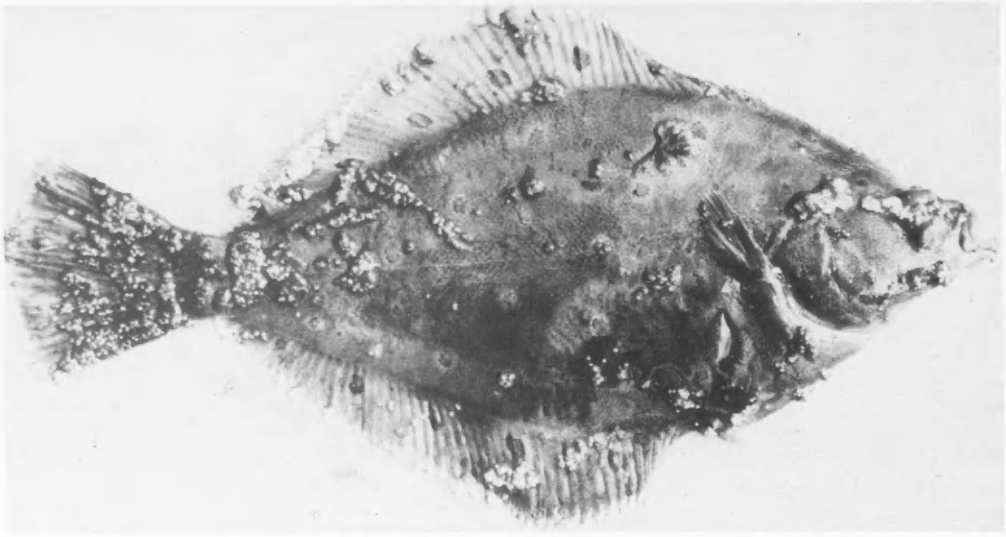

FIGURE 5.—Lymphocystis in European plaice, *Pleuronectes platessa*. (Photograph courtesy of P. Van Banning, Rijkinstituut voor Visserijonderzoek, IJmuiden, Netherlands.)

plaice, *Hippoglossoides platessoides*, from the Grand Banks of Newfoundland. He suggested several possible explanations for the outbreak, including the possibility that the disease is enzootic in the population and may increase in intensity periodically. Earlier, Awerinzew (1911) found annual lymphocystis prevalences of 11% in *P. flesus* from the Murmansk coast, and Nordenberg (1962) found infections as high as 12% in the same species from the Öresund, with some indication of higher prevalence in the warmer months of the year. None of these outbreaks seems to have any apparent association with environmental contamination.

Lymphocystis has been reported recently in Baltic herring (*Clupea harengus* var. *membras*) by Aneer and Ljungberg (1976). Of the 2,629 individuals examined, 14 had gross signs of the disease. The authors pointed out that a number of infections were slight and might easily have been overlooked. It is quite likely that this is the case with other species also.

The presence of lymphocystis cells in the viscera of herring was noted by Aneer and Ljungberg, and there are several other reports of systemic lymphocystis infections, particularly that of Dukes and Lawler (1975) in which lymphocystis cells were found in and behind the eyes and in the kidney, spleen, liver, heart, ovaries, and mesenteries of silver perch, *Bardiella chrysura*, from the Mississippi coast.

Lymphocystis has also been recognized in 4.3% of yellowfin sole, *Limanda aspera*, sampled in the Bering Sea by Alpers et al. (1977a) and in 68% of winter flounder sampled in 1975 from Casco Bay in the Gulf of Maine (Murchelano and Bridges 1976).

Despite inconclusive attempts to relate lymphocystis epizootics in flatfish to specific environmental factors, including pollutants, there are recent observations of the disease in fishes of the Gulf of Mexico that reopen the issue. Christmas and Howse (1970) found lymphocystis in Atlantic croaker and sand seatrout, *Cynoscion arenarius*, from the Mississippi coast of the Gulf of Mexico and observed that "The pollution load was much greater in estuarine systems where lymphocystis was encountered." However, only 12 infected fish were found in a 10-mo trawling survey with monthly collections at 35 stations, which is not overwhelming evidence for a relationship of the disease to pollution. In a later study, Edwards and Overstreet (1976) reported marked increases in lymphocystis incidences in Atlantic croakers from the Mississippi coast, with as high as 50% infected fish in some trawl collections. Increased prevalences of another strain of lymphocystis were also observed in silver perch. In a later paper Over-

street and Howse (1977) stated that (with reference to the silver perch strain) "prevalence appears to relate to rainfall, suggesting that toxicants, salinity, or enriched water could play a major role in infections."

Lymphocystis in striped bass, *Morone saxatilis*, on the U.S. east coast seems to have some tenuous association with heated effluents. Recent unpublished observations by staff members of the Sandy Hook Laboratory (J. S. Young, Fishery Biologist, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732. Pers. commun., September 1975), pointed to high prevalence of lymphocystis disease (Figure 6) in limited samples of striped bass overwintering in the heated effluent of a Long Island generating station (Northport, N.Y.). This disease is considered rare in striped bass (Anonymous 1951; Krantz 1970), and its unusual abundance in a localized population may well be related to the abnormally high winter temperature regime in which the population exists, or to abnormal crowding, with consequent increase in stress and ease of transfer of the pathogen. The high temperature may promote survival or transfer of the pathogen, or lower resistance of the host, or provoke latent infections into patency, resulting in grossly recognizable stages of infection. Lymphocystis is considered to be highly infectious; initial lesions often develop where injuries to the fish have occurred; and lymphocystis virus reaches peak infectivity when water temperatures are high (Midlige and Malsberger 1968). Some or all of these factors may be important in fostering the high prevalences observed in striped bass. An important concern about fish diseases such as lymphocystis in populations overwintering in heated effluents is that a focus of infection will be provided for incoming spring migrants.

STRESS-PROVOKED LATENT INFECTIONS

A number of microbial diseases of fish have been shown to be provoked into patency by environmental stress (Wedemeyer 1970; Snieszko 1974). This seems to be true for kidney disease and furunculosis of salmonids, which often exist in carrier or latent states that can develop into active infections if fish are stressed. It is also probably true for anaerobic bacterial (*Eubacterium* sp.) infections of mullet and 10 other species of fish from Biscayne Bay (Udey et al. 1977). A report of vibriosis in eels held in freshwater (Rødsaether et al. 1977) suggested that latent infections with *Vibrio anguillarum* produced disease and mortalities when eels were exposed experimentally to 30-60 μg/l copper for 50 days in freshwater. Similarly an epizootic of *Aeromonas liquefaciens* (= *A. hydrophila*) in Atlantic salmon, *Salmo salar*, and the sucker, *Catostomus commersoni*, in the Miramichi River, Canada, seemed to be related to combined stresses of copper and zinc pollution and high water temperatures (Pippy and Hare 1969).

FIGURE 6.—Lymphocystis disease in striped bass from heated effluent of a power plant.

Snieszko (1962) stated, concerning *A. liquefaciens* that "... fish may have latent infections that flare up when the fish are exposed to stress."

There are recent published accounts of two viral diseases of marine invertebrates which also indicate that latent infections may be provoked into patency by environmental stress. One, a *Baculovirus* infection of pink shrimp, *Penaeus duororum*, was first recognized in stressed laboratory populations (Couch 1974b, 1976). The other, a herpes-like viral infection of oysters, was discovered in a population held in a heated power plant effluent in Maine (Farley et al. 1972).

An association of shrimp virus disease and low-level chronic exposure to pollutant chemicals is being explored at the Gulf Breeze Environmental Research Laboratory of the U.S. Environmental Protection Agency (Couch 1974a, 1978). In this work a virus disease of pink shrimp caused by *B. penaei* reached patent levels and caused mortalities of 50-80% in shrimp exposed to the PCB Aroclor 1254 and to the organochlorine insecticide Mirex (Couch and Nimmo 1974a, b; Couch 1974a, b, 1976). Other experiments in which the shrimp were crowded, but not exposed to chemicals, resulted in similar enhancement of virus infections, indicating that environmental stress may be an important determinant of patent infections. The virus infection has been found subsequently in brown and white shrimp (Overstreet and Howse 1977; Couch 1978).

Couch and Courtney (1977) have recently proposed an elaborate and unique conceptual scheme to utilize the shrimp virus for interactive bioassays for chronic sublethal effects of contaminants. The authors point out that there are a number of possible interactions of host, pathogen, and chemical stressors—change in resistance of shrimp to the virus, enhancement of widespread latent infections in the shrimp population, change in virulence of the virus, and losses of diseased shrimps by cannibalism. Criteria developed by Couch and Courtney for interaction include increased viral prevalence in stressed populations (as indicated by numbers of inclusion bodies), increased infection intensity in stressed individuals, increased mortality in stressed populations, and greater cytopathic effects in infected and stressed individuals. The shrimp virus infection has great potential for elucidating effects of pollutants on host-pathogen relationships.

An association of high environmental temperatures with high disease prevalence (or disease enhancement) in molluscan shellfish sampled from thermal effluents has been made recently. Farley et al. (1972) described a lethal herpes-type virus disease of oysters held in heated discharge water in Maine. The disease, which apparently existed at a low enzootic level in oysters growing at normal low environmental temperatures (12°-18°C summer temperatures), seemed to proliferate in oysters maintained at elevated temperatures (28°-30°C) and to produce mortalities in those populations. Intranuclear inclusion bodies, containing viral particles, characterized advanced infections. Mortalities of oysters held at higher temperatures were correlated with greater prevalence of the viral inclusions. Elevated water temperatures were considered by the authors to favor spread of the infection or to activate latent infections, or both.

This evidence for a possible role of environmental stress in activating latent viral infections could hardly be termed overwhelming, since it is possible that new infections produce the effects discussed. However, the two viral diseases may provide an insight into the total effect of pollutant and other environmental factors on disease prevalence and disease-caused mortalities. The carrier state is often difficult to diagnose, but it may play a much larger role in the epizootiology of marine disease than can be demonstrated at present.

ENVIRONMENTALLY INDUCED ABNORMALITIES

Neoplasms (Tumors)

The terms "neoplasia" and "neoplasms," particularly as they concern lower animals, are difficult to define precisely. The Oxford Dictionary definition of neoplasm is "a new formation in some part of the body; a tumor." More elaborate definitions exist. Warren and Meissner (1971) defined a neoplasm as "a disturbance of growth characterized primarily by an unceasing, abnormal, and excessive proliferation of cells." Prehn (1971) defined neoplasia as "that form of hyperplasia which is caused, at least in part, by an intrinsically heritable abnormality in the involved cells." Although neoplasia has been studied most extensively in humans and laboratory mammals, the existence of tumors in fish and shellfish has been recognized for almost a century (the first oyster tumor, for example, was reported by Ryder in

1887, and Bonnet mentioned thyroid hyperplasia in fish due to iodine deficiency in 1883).

Circumstantial evidence associating environmental contamination with neoplasms (tumors) in fish has accumulated from a number of studies:

1. Lucké and Schlumberger (1941) described 166 catfish (*Ameiurus nebulosus*) with epitheliomas of lips and mouth, taken from the Delaware and Schuylkill Rivers near Philadelphia. The rivers were grossly polluted. Tumors of this type may result from mechanical, infectious, or chemical irritation. Catfish from other areas did not have a high prevalence of tumors. The authors did not exclude the possibility that the lesions were induced by chemical carcinogens in the water. The lesions developed into epidermoid carcinomas, some of which were invasive.
2. Russell and Kotin (1957) found 10 of 353 white croakers, *Genyonemus lineatus*, from Santa Monica Bay, Calif., with papillomas of lips and mouth. Fish were taken 2 m from an ocean outfall. No tumors were found in 1,116 croakers from unspecified nonpolluted waters 70 km away.
3. Cauliflower disease (epidermal papilloma) has been increasing in prevalence in eels (*Anguilla anguilla*) from the Baltic since 1957. The pattern of spread and high prevalence indicates an infectious process (viral arrays have been seen) or progressive accumulation of industrial contaminants such as fuel oil and smelter wastes (known to contain carcinogenic hydrocarbons such as benzopyrene and heavy metals such as arsenic).
4. Cooper and Keller (1969) reported that 12% of nearly 16,000 English sole from San Francisco Bay had epidermal papillomas, with as many as 33 tumors per fish. Incidence of tumorous fish in the northern part of the Bay was twice that in the southern part. The greatest concentration of industrial waste discharge, especially petrochemicals, existed in the northern part of the Bay. A later survey (Kelly 1971) failed to confirm the areal difference in tumor abundance.
5. Young (1964) found many small (10-15 cm) Dover sole from Santa Monica Bay with tumors. Fish above 15 cm did not have tumors. According to Young, numerous white croakers from Santa Monica and Los Angeles-Long Beach were found with papillomas of the lips, and papillomas were observed on tongue soles, cusk eels, and Pacific sanddabs. Such tumors were not seen by Young on fish from unpolluted areas, but Dover sole with epidermal papillomas have since been collected off Baja California as far south as Cedros Island (Sherwood and Mearns 1976). The prevalence of lip tumors in white croakers from Santa Monica and the Palos Verdes shelf has been <1% since 1970 (Mearns and Sherwood 1977).
6. Carlisle (1969) found "growths" frequent on white croakers and Dover sole from Santa Monica.
7. Sindermann (1976) found wartlike tumors histologically resembling fibromas in *Mugil cephalus* from Biscayne Bay in 1969-70 (Figure 7). Other fibrous tumors have been reported since then by Lightner (1974) and Edwards and Overstreet (1976) in mullet from the Gulf of Mexico.

From the foregoing, it is apparent that much attention has been given, and continues to be given, to the common occurrence of epidermal papillomas in a number of Pacific flatfishes (Wellings et al. 1964, 1965; Wellings 1969a, b). The tumors of English sole from the Pacific coast, for example, have been studied for almost half a century (Pacis 1932; McArn et al. 1968; Good 1940; Angell et al. 1975). Stich et al. (1976) in their review of fish tumors and sublethal effects of pollutants, found highest prevalences to occur in young-of-the-year fish. Maximum prevalences reported in the literature were 58% in English sole (Stich and Acton 1976); 55% in starry flounder (McArn and Wellings 1971); 15% in flathead sole, *Hippoglossoides elassodon* (Miller and Wellings 1971); and over 40% in sand sole, *Psettichthys melanostictus* (Nigrelli et al. 1965). A relationship of high frequencies of such papillomas with coastal pollution is still uncertain. Stich et al. (1976) stated "There seems to be a higher skin tumor frequency among English sole inhabiting areas of urban contamination (Vancouver) than among fish populations in regions remote from human activities . . . ."

In an extension of this study, Stich et al. (1977) reported prevalences of skin neoplasms in 1-yr-old English sole of from 20 to 70% in samples taken near eight cities on the Pacific coast, while prevalences did not exceed 0.1% in several samples taken on the British Columbia coast more distant from cities. However, Oishi et al. (1976) examin-

FIGURE 7.—Wartlike fibrous tumors in *Mugil cephalus* from Biscayne Bay, Fla.

ing prevalences of similar epidermal papillomas in flatfish from relatively unpolluted waters of northern Japan felt that a possible association existed between high tumor occurrence (up to 20% in certain samples) and parasitization of the flesh by a nematode, *Philometra mariae*, but then they suggested that the involvement of naturally occurring chemical contaminants as well as man-made pollutants must be considered in the etiology of flatfish neoplasms.

Wellings et al. (1977) found 1.0% of rock sole, *Lepidopsetta bilineata*, sampled in the still-unpolluted Bering Sea, with epidermal papillomas. Infections were widely distributed geographically, mostly in older individuals. The age distribution of infection was quite different from that in Puget Sound flatfishes, where predominantly younger fish are involved.

The etiology of skin tumors in English sole from the Pacific coast of North America was reviewed in a recent paper by Angel et al. (1975), with the conclusion that the cause is unknown, and may be multifactorial. Three stages of tumorigenesis were described in young-of-the-year English sole, beginning with angioepithelial nodules and progressing to epidermal papillomas and angioepithelial polyps. No conclusive role of an environmental carcinogen has been demonstrated; there seem to be subpopulation differences in disease prevalences; and electron microscopy has disclosed the presence of viruslike particles in cells of papillomatous fish (Wellings and Chuinard 1964), but attempts to isolate a viral agent have been unsuccessful.

To further complicate the story, an unknown cell type, called an "X cell," has been found in all three tumor stages in English sole. The cells may be parasitic, as was suggested by Brooks et al. (1969), and Alpers et al. (1977b), or they may be transformed host cells, analogous to lymphocystis cells, as was suggested by Angell et al. (1975). Angell et al. concluded by stating that "given the pervasiveness of certain pollutants, experimental evidence and further field studies will be necessary to clarify the relationship between tumorous flatfishes and pollution."

Another observation on the possible relationship of flatfish tumors and pollutants has been supplied by Mearns and Sherwood (1974). The distribution and abundance of skin tumors and fin

erosion were studied simultaneously in Dover sole from the California coast. Fin erosion was more common in specimens collected near major sewer outfalls, whereas tumorous fish were distributed more evenly throughout southern California coastal waters. The authors concluded that "The spatial and temporal distribution of tumor-bearing Dover sole suggest that initiation of the disease was not related to [municipal] wastewater discharges [in southern California]."

A recent report of neoplasms in the Atlantic hagfish, *Myxine glutinosa*, by Falkmer et al. (1977) suggested a possible relationship of PCB contamination and tumor prevalence. During a 5-yr (1972-76) study in Gullmar Fjord, Sweden, neoplasm prevalences, particularly hepatomas, decreased from 5.8 to 0.6%. PCB levels in livers of hagfish were appreciable (5 ppm), but the use of PCB was prohibited in 1971. Liver PCB levels in hagfish caught inside the fjord were five times higher than in those caught outside. However, the association of PCB contamination with liver tumors must be considered to be tenuous. Earlier reports of neoplasms in hagfish (Fänge et al. 1975; Falkmer et al. 1976) described remarkably high frequencies in Gullmar Fjord, but only low concentrations (0.5-1.0 ppm) of PCB in livers, and low environmental levels of PCB and other contaminants.

The role of environmental chemical factors in induction of neoplasms in shellfish is even less clear than for fish, but there is some limited information. Yevich and associates (Barry and Yevich 1975; Yevich and Barszcz 1976, 1977) have for a number of years examined the occurrence of neoplastic growths in the soft-shell clam, *Mya arenaria*, in relation to petroleum contamination. Gonadal and hematopoietic neoplasms were observed in animals collected from two chronically contaminated sites on the Maine cost, with prevalences up to 29% in certain samples. Yevich and Barszcz (1976) stated that "no tumors similar to those described [from the petroleum contaminated area] have been encountered in animals collected from any other area." They described the scope of their study as "several thousand animals from all coastal areas of the United States." Additional samples of clams from a number of other coastal locations are needed, as is a more precise description and confirmation of the neoplastic condition.

It is interesting that a counterpart study of soft-shell clams from Rhode Island and Massachusetts (Brown et al. 1976) reported occurrences of neoplasia, apparently of hematopoietic origin, in up to 26%, with the highest frequency in samples from a 1975 oil spill area near Bourne, Mass. A later report (Brown et al. 1977) included additional samples from other geographic areas. Neoplasms of gonadal origin, similar to those reported by Yevich and associates, were found in clams from an oil-contaminated site at Searsport, Maine. The highest prevalence of neoplasms of hematopoietic origin was 64%, in a small sample from Bourne. The authors pointed out, however, that clams from some oil-contaminated sites had no neoplasms, and stated that "These results suggest that the type and degree of hydrocarbon pollution are possibly related to the frequency of neoplasms and other lesions in *Mya*, but they are by no means the only causative factors."

Other types of cellular abnormalities have been reported from soft-shell clams. In earlier studies by Yevich and associates (Barry et al. 1971) atypical epidermal hyperplasia in gills and kidney was reported in up to 40% of clams sampled near Providence, R.I. Lesions occurred more frequently in large individuals, and seasonal changes were not observed. Lower prevalences were found in limited samples from Maine, Maryland, and California. Unlike the oil spill studies, no association with environmental factors was made by the authors.

Yevich and associates (Yevich and Barry 1969; Barry and Yevich 1972) have also described gonadal neoplasms in quahogs, *Mercenaria mercenaria*, from Narragansett Bay. Samples collected in 1968, 1969, and 1970 had tumor frequencies of 0.2, 2.3, and 2.7% respectively.

Epizootic neoplasms with a possible environmental etiology were reported from several molluscan species of Yaquina Bay, Oreg. (Farley 1969b; Farley and Sparks 1970; Mix et al. 1977). Blue mussels, *Mytilus edulis*, native oysters, *Ostrea lurida*, and two species of *Macoma* were affected, and winter mortalities were associated with the disease. Neoplasms have not been found in bivalve molluscs sampled elsewhere on the Oregon coast (Mix et al. 1977).

In another study (Christensen et al. 1974) similar epizootic neoplasms (up to 10% prevalence) were found in a localized population of the clam *Macoma balthica* from a tributary of Chesapeake Bay. The neoplasms were invasive and systemic, with initial foci in the gill epithelia. Holding experiments indicated that the disease was usually

fatal. The authors suggested, but did not demonstrate, an environmental contaminant etiology, possibly associated with bottom detritus. Other bivalve molluscs in Chesapeake Bay contain neoplasms. American oysters, *Crassostrea virginica*, were found with hematopoietic neoplasms (Farley 1969a; Couch 1969, Frierman 1976), and individual oysters have been reported to contain other types of neoplasms (Pauley 1969; Couch 1970).

Much of the evidence associating certain neoplasms of fish and shellfish with pollutants should be considered as circumstantial but provocative (Rentchnick 1976). Many of the neoplasms have been reported from bottom-feeding fish and detritus or filter-feeding bivalves, as was pointed out by Harshbarger.[9] Chemical carcinogens such as certain heavy metals and hydrocarbons can be concentrated in surficial layers of bottom sediments and can thus be readily available to animals inhabiting that zone. It should be noted, though, that a number of recent studies of neoplasms in fish and shellfish have found no obvious relationship between neoplasms and specific environmental factors.

Skeletal Anomalies

Skeletal anomalies, particularly those of the spinal column, are commonly observed in fish and are the subject of an extensive literature (see Hickey 1972, for a recent summary and Dawson 1964, 1966, 1971, and Dawson and Heal 1976 for a complete bibliography).

Such anomalies may be genetic, resulting from mutations or recombinations; epigenetic, acquired during embryonic development; or postembryonic, acquired during larval development, at metamorphosis, or during juvenile development (Hickey 1972). Spinal flexures and compressions, as well as vertebral fusions, have been observed in many teleost species, as have head and fin abnormalities. Evidence exists for a hereditary basis for some skeletal anomalies (Gordon 1954; Rosenthal and Rosenthal 1950), but other evidence points to effects of environmental factors such as temperature, salinity, dissolved oxygen, radiation, dietary deficiencies, and toxic chemicals. For example, increased percentages of abnormal embryos and larvae of Atlantic herring, *Clupea harengus*, resulted from experimental exposures to sulfuric acid waste water (Kinne and Rosenthal 1967) and to the algicides 2,4- and 2,5 dinitrophenol (Rosenthal and Stelzer 1970).

Recently, increased prevalences of skeletal deformities and anomalies, considered to be pollution-associated, have been recognized in a few fish species from southern California, the British Isles, and Japan. In studies carried out in California, skeletal deformities occurred with greater frequency in samples from areas with significant pollutant stress (Valentine and Bridges 1969; Valentine et al. 1973). Exposure of fry to very low concentrations of DDT (<1 ppb) produced anomalies in fin rays (Valentine and Soulé 1973).

Probably the most convincing observational evidence for environmental influences on induction of skeletal abnormalities in marine fish is that presented by Valentine (1975). Examining samples of barred sand bass, *Paralabrax nebulifer*, Valentine found significantly higher prevalences of anomalies, particularly gill raker deformities, in fish from the southern California coast (Los Angeles and San Diego) than from the Baja California coast. The anomalies increased in frequency and severity with increasing size of the fish and an association with disturbed calcium metabolism was suggested. The author pointed to the high chlorinated hydrocarbon and heavy metal levels which characterize the California coastal area (Schmidt et al. 1971; Galloway 1972), but emphasized that a causal relationship with increased prevalence of anomalies had not been established. However, Valentine's suggestion of a possible causal relationship between high environmental levels of chlorinated hydrocarbons and heavy metals, both of which are known to interfere with calcium metabolism, and skeletal anomalies in fish seems reasonable, in view of experimental evidence from a wide range of vertebrates (Ferm and Carpenter 1967; Lehner and Egbert 1969; Peakall and Lincer 1970; Pichirallo 1971; McCaull 1971; Galloway 1972).

Valentine (1975) referred briefly to additional observations on two other Pacific coastal species—California grunion, *Leuresthes tenuis*, and barred surfperch, *Amphistichus argenteus*—in which gill raker anomalies increased in frequency with age, and were "virtually restricted to [samples from] fishes from Southern California." This finding in three species reduces the likelihood that frequency differences could be attributable to

[9]Harshbarger, J. C. 1974. Activities report (of the) registry of tumors in lower animals 1965-1973. Smithson. Inst., Wash., D.C., 141 p.

inherited subpopulation differences in one of the three species studied.

While the deformed gill rakers were the most prevalent anomalies observed in southern California barred sand bass by Valentine, other abnormalities (pugheadedness, cranial asymmetries, deformed vertebrae, and fin anomalies) occurred and were associated directly in frequency and severity with gill raker deformity.

An analysis of vertebral deformities in herring taken in waters around the British Isles (van de Kamp[10]) indicated a slight but significant increase in prevalences from 1960 to 1975. The predominant abnormality was a cluster of two or three incomplete vertebrae located near the pelvic fins or anus. The highest percentages of abnormalities were found, according to the author, in areas "which probably had the highest degree of pollution." It was in these areas where prevalences also showed slight increases during the study period, supporting the author's hypothesis that vertebral deformities in herring can be related to "unusual substances" in the environment. However, van de Kamp concluded by stating that more experimental work on the causal relationship between pollution and deformities will be required.

Several reports from Japan refer to high and increasing occurrences of skeletal anomalies in fish. Komada (1974) and Ueki and Sugiyama (1976) observed increasing numbers of malformed sweetfish or ayu, *Plecoglossus altivelis*, in rivers and culture farms. Skeletal abnormalities in mullet and eight other species from the Inland Sea of Japan were reported by Matsusato (1973).

Deformed fin rays (Figure 8) and associated skeletal abnormalities have been observed repeatedly in winter flounders from the highly polluted waters of the New York Bight (Ziskowski et al. in press), and a summarization of observations on skeletal anomalies and related developmental defects has been published recently (Sindermann et al. 1978).

There is some evidence from studies of a few other fish species for an involvement of various kinds of environmental stress in the occurrence of skeletal anomalies. Gabriel (1944) noted anomalies in vertebrae of *Fundulus heteroclitus* due to temperature changes, and Mottley (1937) found anomalies in vertebral numbers of trout due to temperature (and possible oxygen). Hubbs (1959) found high prevalences of vertebral abnormalities in mosquitofish, *Gambusia affinis*, from Texas warm springs and concluded that the high temperature was responsible.

There is also an appreciable literature concerned with induction of skeletal injuries in fish by exposure to contaminants. Vertebral damage following experimental exposure to aquatic contaminants has been reported for a number of freshwater fishes (Bengtsson 1975). Long-term (10 wk) exposure of minnows (*Phoxinus phoxinus*) to sublethal concentrations of zinc and cadmium resulted in hemorrhaging, spinal curvatures, and vertebral fractures, particulary in the caudal region, in up to 70% of individuals. Spinal curvatures and muscle atrophy were produced in rainbow trout by chronic exposure to lead. It is interesting that caudal fin erosion was also observed in these experiments. In earlier studies, summarized by Bengtsson, exposure to sublethal concentrations of the chlorinated hydrocarbon Toxaphene as well as to Malathion, parathion, and certain other organophosphorus pesticides produced vertebral damage or spinal flexures in several fish species. Vertebral damage was considered to have a neuromuscular origin, or, in the case of long-term exposure, to be a consequence of demineralization.

John Couch and associates at the Gulf Breeze Environmental Research Laboratory of the U.S. Environmental Protection Agency are developing experimental evidence for induction of skeletal abnormalities by exposure to environmental contaminants. Couch et al. (1977) reported severe scoliosis and associated pathology in the sheepshead minnow, *Cyprinodon variegatus*, exposed to the organochloride pesticide Kepone. The authors concluded that scoliosis was a secondary effect of Kepone toxicity, with the nervous system or calcium metabolism as the primary target.

Couch and associates (J. A. Couch, Research Pathologist, Environmental Research Laboratory, U.S. Environmental Protection Agency, Gulf Breeze, FL 32561. Pers. commun., June 1977) have also found that trifluralin (Treflan) induced extensive osseous hyperplasia in vertebrae of sheepshead minnows when life history stages from zygote to 28-day juveniles were exposed to 25-50 ppb trifluralin. Centra of vertebrae, thickened by active osteoblasts and fibroblasts, increased in size up to 10-30 times their normal dimensions—a striking sublethal effect.

[10]van de Kamp, G. 1977. Vertebral deformities in herring around the British Isles and their usefulness for a pollution monitoring programme. Int. Counc. Explor. Sea, Fish. Improv. Comm., Doc. CM1977/E:5, 9 p.

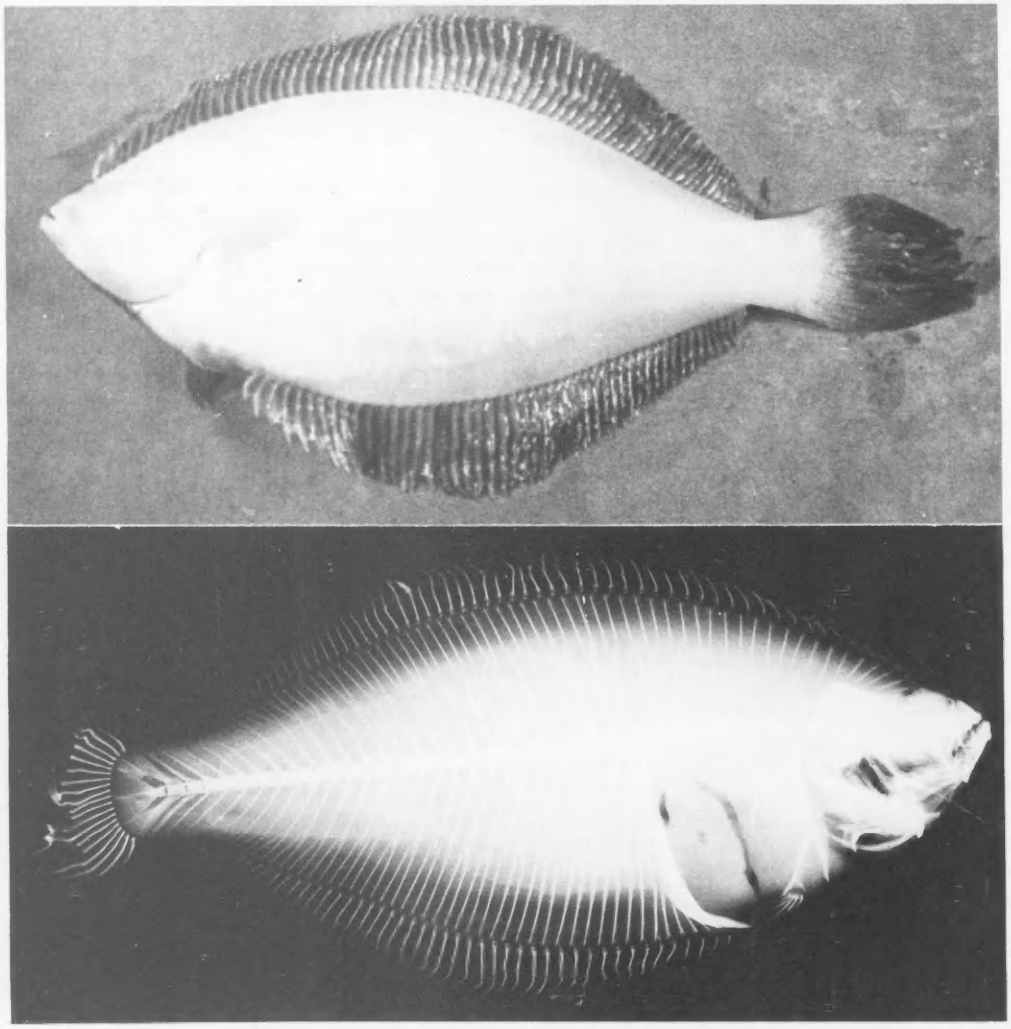

FIGURE 8.—Deformed fin rays in winter flounder from New York Bight. External appearance (above) and radiograph (below). (From Sindermann et al. 1978.)

GENETIC ABNORMALITIES

The mutagenic properties of a number of chemical contaminants including heavy metals, pesticides, and petroleum-derived polycyclic hydrocarbons have been demonstrated in experimental studies with terrestrial animals (Huberman 1975; Longwell[11]). Fish eggs can be vulnerable to contaminant effects from the body burden of the parent female and from exposure to contaminants in surface water and/or sediments (depending on where in the water column spawning and development occur). Sperm cells are sensitive to contaminants, and eggs are especially sensitive during meiosis and early cleavage stages. Furthermore, chemical mutagens can reduce the rate

[11]Longwell, A. C. 1975. Mutagenicity of marine pollutants as it could be affecting inshore and offshore marine fisheries. Middle Atl. Coastal Fish. Cent., Natl. Mar. Fish. Serv., Inf. Rep. 79, 72 p.

of cell division and can damage the mitotic spindle apparatus. Pelagic eggs may be most severely damaged, since the surface film of the ocean has been found to contain high concentrations of contaminants such as petroleum components, halogenated hydrocarbons, and heavy metals (MacIntyre 1974).

Some experimental evidence is available. Fish larvae incubated in cadmium-polluted water accumulated the metal (Westernhagen et al. 1974; Rosenthal and Sperling 1974), and eggs incubated in as little as 1 ppm cadmium produced low percentages of viable larvae (Westernhagen et al. 1975; Westernhagen and Dethlefsen 1975).

Some relevant experimental research on radionuclide-induced mutagenesis (Romashov and Belyayeva 1966; Ivanov 1967; AEC-TR-7299[12]) has disclosed that many fish embryos with severe chromosomal damage died during the transition from blastula to gastrula. Abnormal postgastrula embryos contained higher numbers of chromosomal aberrations than normal embryos, and the abnormal embryos had high mortality just before hatching. However, even the normal-appearing embryos with radiation exposure (and consequent genetic disturbances) had low viability and high mortality at hatching and subsequent to hatching.

Recently, Longwell (1976a, b) reported high prevalences of chromosomal anomalies in Atlantic mackerel, *Scomber scombrus*, eggs and embryos in certain samples taken from the New York Bight. All degrees of chromosomal damage were found, including failure to align at the metaphase plate, incomplete spindle formation, translocation bridges, chromosomal "stickiness," losses of portions of chromosomes and "pulverization." Eggs with at least one chromosome or mitotic abnormality varied from 13 to 79%. Higher percentages seemed associated generally with degrees of environmental degradation. In addition to chromosomal anomalies, one station (the one with highest prevalence of anomalies) was also characterized by significant (26%) egg mortality.

The techniques developed by Longwell (1976b) permitted examination of historical collections of eggs and embryos for chromosomal damage. A limited collection taken in 1966 from the same geographic area disclosed a lower incidence of cytogenetic abnormalities than that found in the 1974 collection.

Samples examined to date from normal and degraded waters are still insufficient, as Longwell (1976b) pointed out, to make definitive statements about the relationship of pollutants and extent of damage to genetic material, but the data presented so far indicates that such a relationship may exist. Because of the implications of these findings in survival and abundance of economic marine species, it is particularly important that this kind of research be pursued vigorously. It may well be that a new and significant mortality factor for estuarine and coastal populations—increased genetic damage—may have been introduced with increasing chemical pollution.

It is likely that marine organisms will respond to mutagens in species-specific ways and with differing sensitivities. Some indication of this can be found in a recent paper by Vandermeulen and Lee[13] in which cultures of the alga *Chlamydomonas reinhardtii* were exposed to crude and refined oils (Kuwait crude, Saran Gach crude, diesel 25, and bunker C). No enhanced mutation rates (as detected by streptomycin resistance) were found after 3 wk of exposure (40-50 generations), a surprising finding, since the alga is susceptible to certain other known mutagens and since the test oils contain various polycyclic aromatics which are known mutagens. No cytological examinations were reported. The authors pointed out that concentrations of mutagenic components in the test oils may be low compared with concentrations used in cell and tissue culture to elicit enhanced mutation rates, and that extrapolation of laboratory results to the marine environment should be done very conservatively.

An indirect test for the presence of mutagens in the marine environment has been reported recently by Parry et al. (1976). *Mytilus edulis* were sampled from polluted and unpolluted waters of the United Kingdom, and extracts of their tissues were tested for ability to induce genetic changes in bacterial and yeast cultures. Significant increases in mutation rates for specific gene loci characterized cultures exposed to extracts of mussels from polluted waters, but not those from clean waters—providing evidence for the presence of mutagens that had been concentrated in the tis-

[12]AEC-TR-7299. Marine radioecology. 1972. (Distributed by NTIS, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, VA 22151.)

[13]Vandermeulen, J. H., and R. W. Lee. 1977. Absence of mutagenicity due to crude and refined oils in the alga *Chlamydomonas reinhardtii*. Int. Counc. Explor. Sea, Plankton Comm., Doc. CM1977/E:69, 5 p.

sues of mussels from polluted areas. The chemical nature of the mutagens was not identified, except that the mussels came from areas with heavy industrial pollution.

EXPERIMENTALLY INDUCED LESIONS

There is a vast and almost unmanageable amount of published information about the induction of various lesions in fish by experimental exposure to chemical contaminants (see for example Ribelin and Migaki 1975). A "lesion" may be defined generally as "any localized abnormal structural change in the body." Such a definition obviously includes too much, so the term can be reduced to encompass "those cellular and tissue changes, demonstrable histologically, that result from a disease process." Histopathology of fish and shellfish is still a developing science, and as such it still draws from human and veterinary (mammalian) pathology for its concepts and much of its terminology. Histopathology has been a basic tool in human medicine for some time, and a large amount of information is available about cellular responses to toxicants. A similar core of knowledge is being developed for fish and shellfish—relating cell and tissue changes to kinds and amounts of contaminants.

Early experimental exposures of estuarine and marine animals to contaminants usually had the purpose of determining lethal dosages, either from acute or chronic exposures. More recently, attention has been redirected to sublethal toxic effects—expressed in behavioral, physiological, or cytological responses to specific contaminants. An extensive literature exists concerning cell and tissue damage resulting from experimental exposure to contaminant chemicals. Generalizations that can be made are almost predictable: 1) increasing dosages, beyond a threshold level, produce increasingly severe tissue abnormalities; 2) particular contaminants often exert effects on specific target tissues; 3) principal target tissues seem to be gill epithelium, liver (or in the invertebrate, the hepatopancreas), and neurosensory cells; 4) specific lesions cannot usually be described as characteristic of any group or class of chemicals; and 5) effects that may be of chemical origin can be obscured by stress-provoked infections with facultative pathogens. Some information about experimental induction of fin erosion and skeletal abnormalities has been included in earlier sections of this paper, but because of the sheer volume of published information about other types of experimental lesions, it seems worthwhile to summarize some of the observations here.

Couch (1975) published a recent and excellent review of the histopathological effects of pesticides and related chemicals on the livers of fishes. The liver and fatty tissues of fish from natural waters are known to accumulate a number of chlorinated hydrocarbons (Duke and Wilson 1971), and experimental exposures of fish to pesticides result in high concentrations and greatest effects on the liver (Johnson 1968; Eisler and Edmunds 1969; Hansen et al. 1971; Eller 1971). Some of the observed liver histopathology includes:

Chlorinated hydrocarbon pesticides: Focal areas of parenchymal cell vacuolation and degeneration (Eller 1971), inflammation, and loss of glycogen and fat (Lowe 1965).

Clorinated hydrocarbon herbicides: Increase in connective tissue, massive focal necrosis (Cope et al. 1969), and loss of glycogen (Cope et al. 1970).

PCB's: Focal degenerative regions, parenchymal cell vacuolation and pleomorphism (Eller[14]), lipid accumulation in hepatic cell vacuoles, and leucocytic infiltration (Couch 1975).

Organophosphates: Edema, hyperemia, vacuolation, and necrosis of parenchymal cells (Eller, see footnote 14).

Carbamates: Hypertrophy and vacuolation of acinar cells (Couch 1975).

It should be noted that not all experimental exposures to pesticides, even for prolonged periods, necessarily caused demonstrable tissue pathology, but in many instances additional exposure experiments are needed (even though the literature as summarized by Couch (1975) seems voluminous). Couch pointed out that over 900 commercial pesticide formulations are in general use, and of these fewer than 30 have been tested for pathological effects on livers of fishes.

Pesticides can, of course, affect fish tissues other than liver. A summarization of general histopathological effects of pesticides on fish was published by Walsh and Ribelin (1975). Data from their own studies with coho salmon, *Oncorhynchus kisutch*, and lake trout, as well as from other

[14]Eller, L. L. 1970 and 1971. Annual reports. U.S. Bur. Sport Fish. Wildl., Fish Pestic. Lab., Columbia, Mo.

published work, led them to the conclusion that tissue changes observed as a result of exposure to an array of common pesticides were largely nonspecific, and therefore of limited diagnostic value. Their attempts to identify specific lesions as characteristic of any group or class of pesticides were described by them as "futile," but the amount of histopathological information presented in the paper is substantial, and their summarization of pathology produced by exposure to widely used pesticides is instructive.

DDT: Necrosis of hepatic cells; lymphocytic infiltration of intestinal lamina propria; possible degeneration of kidney tubules.

Carbaryl (Sevin): Intramuscular hemorrhages adjacent to vertebral column; atrophy of the lateral line musculature; myxomatous degeneration of fat; vacuoles within the optic tectum of the brain.

Malathion: Subcutaneous hemorrhages at the bases of pectoral fins.

Endosulfan (Thiodan): Hyperemia of intestine and brain; adrenal cortical hyperplasia.

2,4-D: Striking degree of brain hyperemia; hyperemia of intestine.

Atrazine: Marked edema of all tissues; changes in skin pigmentation.

It is interesting that Walsh and Ribelin (1975) (unlike Couch 1975) found liver changes in fish exposed to pesticides ". . . minimal and diagnostically unimportant . . . ." They also considered gill epithelial hyperplasia, gill hemorrhages, and lymphocyte reduction in the spleen to be nonspecific responses to stress and/or infection. They further pointed out that rapid autolysis of fish tissues after death rather than direct effects of pesticides might account for some reported histopathological findings. These are all points of importance in evaluating histological findings after exposure to any contaminant.

There are still other histopathological studies of the effects of pesticides on fish that disclose damage to neurosensory tissue. Epithelial necrosis was found in lateral line canals of killifish, *Fundulus heteroclitus*, that survived 96-h exposures to the chlorinated hydrocarbon methoxychlor at 25 mg/l (Gardner 1975). No damage to the mechanoreceptors was evident, but the radius of the canal lumina was reduced.

Pesticides can produce tissue pathology in invertebrates as well. Oysters exposed chronically to 3 ppb DDT, Toxaphene, and parathion exhibited variable lesions, including leucocytic infiltration or hyperplasia of the gonadal germinal epithelium, necrosis of digestive tubule epithelium, and edema (Lowe et al. 1971). In another study, chronic exposure of oysters to 5 ppb PCB produced atrophy of digestive epithelium, leucocytic infiltration, and degeneration of vesicular connective tissue (Lowe et al. 1972). Gill edema and progressive necrosis of filaments in the crustacean *Gammarus oceanicus* resulted from exposure to sublethal concentrations of PCB (Wildish 1970). Examination of pink shrimp, exposed experimentally to PCB's, disclosed a variety of nonspecific tissue changes, especially in the hepatopancreas (Couch et al. 1974). Histological changes included lysis of hepatopancreatic epithelium, nuclear pycnosis, vacuolization of secretory cells, and a variety of ultrastructural changes in absorptive cells.

The literature on experimentally induced lesions in estuarine/marine fish caused by exposure to heavy metals was reviewed recently by Gardner (1975) in a paper which also presented significant new information. His general conclusion was that sensory organ systems of some species are vulnerable to copper, mercury, and silver. Short-term exposure of the killifish to sublethal concentrations of copper resulted in degeneration of anterior lateral line and olfactory sensory tissues (Gardner and LaRoche 1973). Prolonged exposure to copper (copper chloride) resulted in hyperplasia or necrosis of sustentacular epithelium of the olfactory organs and necrosis of the epithelial lining of olfactory pits. Mercury (mercuric chloride) also produced severe degenerative changes in cells of the lateral line canals and olfactory organs of killifish, but without associated necrosis of supporting tissues. Exposure to silver produced histopathological changes very similar to copper. Cadmium (cadmium chloride), however, did not seem to affect the sensory tissues discussed above, at least in terms of causing demonstrable tissue changes. Cadmium exposure did result in transient thyroid hyperplasia and altered blood cell ratios in long-term exposures.

Experimental exposure of the cunner, *Tautogolabrus adspersus*, to cadmium caused pathological changes in kidney, intestine, hemopoietic tissue, epidermis, and gills (Newman and MacLean 1974). Necrosis of tubular epithelium of the kidney, sloughing of intestinal epithelium, hypertrophy and hyperplasia of gill epithelium, and decrease in mucus secretion were

the principal histopathologic findings. Mortality following acute exposures was attributed to renal failure. These results were similar in most respects to cadmium-induced pathology in killifish, reported earlier by Gardner and Yevich (1970).

Experimental cadmium exposures can cause gill lesions in shrimp, as reported in recent papers by Nimmo et al. (1977) and Couch (1977). Exposure of pink shrimp to 763 μg/l of cadmium for 15 days resulted in a "black gill" condition characterized by necrosis of all cell types in the distal gill filaments, with coincident appearance of black granules in the cytoplasm, and some hemocyte infiltration at the bases of the necrotic filaments. Couch suggested that the black deposits could be a metallic sulfide or even cadmium. He further pointed out that the distal filament tissue has been postulated to have detoxifying, as well as osmoregulatory and respiratory functions, so that cell death could result from cadmium filtration and accumulation as part of a detoxification process.

Zinc has been shown to be toxic for fish (see reviews by Skidmore 1964, 1970). Gill tissues can be destroyed in acute exposures, while chronic levels induce stress which may result in mortality and may also produce severe degenerative changes in the liver and kidneys (Crandall and Goodnight 1963). Synergistic activity of zinc with a wide range of environmental variables—other contaminant heavy metals, low dissolved oxygen, and temperature—has been demonstrated for a number of fish species (Doudoroff 1957; Lloyd 1960, 1961a, b). Resistance to zinc poisoning varies with individuals, with age, with degree of acclimatization, and with species (Jones 1938, 1940).

Histopathological effects of sublethal concentrations of copper on the winter flounder were described by Baker (1969). At dosages of 1,000-3,200 μg/l, the kidney hemopoietic tissue became necrotic; gill epithelium became disoriented; chloride cells increased in number and size; gill lamellar fusions occurred; and fatty metamorphosis of the liver was observed. Experimental concentrations were far above those levels expected in most marine environments (concentrations in polluted waters have been reported to reach 300μg/l by Fujiya (1960)).

An interesting study of pathology in American lobsters was made following disclosure of severe yellow phosphorus industrial contamination of Placentia Bay, Newfoundland (Aiken and Byard 1972). Experimental lobsters, exposed to phosphorus contaminated sediments in aquaria, exhibited degenerative changes in antennal glands and in all cell types in the hepatopancreas, as well as massive coagulation of hemolymph.

Experimental exposure to petroleum components and residues may also induce histopathological changes in fish. Hyperplasia of the olfactory sustentacular epithelium and degeneration of the olfactory mucosa of the Atlantic silverside, *Menidia menidia*, resulted from exposure to crude oil (Gardner 1975). Additionally, degeneration of the ventricular myocardium of the heart and pseudobranch secretory cells was seen. Soluble components of the crude oil also caused epithelial metaplasia, replacing the sensory epithelium of the olfactory organs by poorly defined cell types (Gardner 1975). Liver damage occurred in fish fed cyclopropenoid fatty acids (Malevski et al. 1974), but Brocksen and Bailey (1973) found no histopathology in chinook salmon and striped bass exposed to sublethal concentrations of benzene.

Histopathological effects of petroleum on bivalve molluscs are varied in the extreme. Effects, particularly on gill epithelium, have been observed by Barry et al. (1971), Jeffries (1972), LaRoche (1972), Clark et al. (1974), and Gardner et al. (1975). Fries and Tripp (1976) found damage to gill epithelium in hard (hard-shell) clams, *Mercenaria mercenaria*, exposed to as little as 1 ppm phenol. Vaughan[15], however, found little histopathology after chronic exposures of oysters to No. 2 fuel oil. Stainken (1975) found that exposure of soft-shell clams to No. 2 fuel oil at winter seawater temperatures (4°C) for 28 days had little histopathological effect, beyond signs of starvation (glycogen depletion and vacuolization of digestive diverticula cells), and a generalized leucocytosis, even at 100 ppm. No mortalities occurred, and exposure concentrations dropped rapidly, possibly because much of the oil was trapped in mucus as part of the mucociliary feeding mechanism, and ejected from the clam.

Experimental lesions are instructive in identifying target organs and tissues for particular contaminants, but they have numerous flaws when attempts are made to relate experimental findings to events in the natural (polluted) environment: 1) dosage levels are often beyond

[15]Vaughn, B. E. (editor). 1973. Effects of oil and chemically dispersed oil on selected marine biota - a laboratory study. Am. Pet. Inst. Publ. 4191.

maximum observed environmental levels; 2) usually single chemicals are tested, ignoring possible synergisms and antagonisms; 3) tests are often static acute rather than chronic exposures in flow-through systems; and 4) experimental animals are often under stress from the mere act of confinement.

These and other limitations of experimental studies degrade the evidence obtained to circumstantial when attempts are made to extrapolate findings to natural populations in polluted habitats. Despite this handicap, there is a large and useful literature on experimental lesions in fish and shellfish produced by chemicals which occur as contaminants in the coastal environment.

The presence of specific pollutants cannot be recognized by the occurrence of specific lesions, but a general description of pathological responses can be useful. Categories of pathological responses which should be considered in experimental studies are: 1)inflammation (acute and chronic); 2) degeneration (including edema, necrosis, and metaplasia); 3) repair and regeneration (proliferation, hyperplasia, and scar formation); 4) neoplasia (including consideration of cell origin, stage, and type—whether benign or malignant); and 5) genetic derangement (including chromosomal changes and skeletal abnormalities).

CONTAMINANT EFFECTS ON RESISTANCE AND IMMUNE RESPONSES

Suppression of immune responses by toxicants such as heavy metals and pesticides has been demonstrated repeatedly in mammals (Kolomiitseva et al. 1969; Hemphill et al. 1971; Khan and Hill 1971; Jones et al. 1971; Koller 1973; Street and Sharma 1975). Therefore, it might be expected that environmental pollutants could influence the ability of fish and shellfish to resist infection by reducing the effectiveness of external and internal defense mechanisms, and indeed there is some evidence that this is so. Changes in the principal external defenses—mucus secretion of fish and the epicuticle of Crustacea—have already been mentioned in connection with fin erosion and exoskeletal erosion. Some specific information is available about contaminant influences on internal defenses, principally through suppression of immune responses. Environmental stress from contaminants can affect internal resistance to infection in fish by causing a decrease in phagocytic activity (Wedemeyer 1970) or a decrease in antibody synthesis (Goncharov and Mikyakov 1971). Both mechanisms have been demonstrated experimentally.

One of the best pieces of supporting information about suppression of host responses was derived from a recent multidisciplinary experimental study of the effects of short-term sublethal exposures to cadmium on the teleost *Tautogolabrus adspersus* (Calabrese et al. 1974). The study included chemical analyses of tissue uptake, physiological and biochemical effects, histopathological changes, and effects on the immune system. Robohm and Nitkowski (1974), who were responsible for the immunology, found that exposure of fish to 12 ppm cadmium affected phagocyte response to foreign antigen, but not the humoral response. The rate of bacterial uptake in phagocytes of liver and spleen was increased, but the rate of bacterial destruction within the phagocytes was decreased significantly. No change was observed in the antibody response of immunized control and experimental fish as determined by hemagglutination techniques. The authors postulated that cadmium may prevent delivery of lysosomal substances to the phagocytic vacuole, or may inhibit the action of these substances on bacteria, but that cadmium does not seem to inhibit antibody synthesis by lymphocytic cells. The authors further suggested that cadmium and possibly other pollutants may affect fish populations by causing phagocytic dysfunction, reducing the resistance of fish to facultative and other pathogens.

The effect of sublethal copper exposure on the immume response of juvenile coho salmon, *Oncorhynchus kisutch*, was examined by Stevens.[16] At copper levels of 18 μg/l, agglutinin titers in fingerlings injected intraperitoneally with *Vibrio anguillarum* bacterin were significantly lower than those of controls. Copper exposure also reduced survival of coho salmon fingerlings during saltwater acclimation.

Reduction in immunological competence may well have been involved in observed outbreaks of vibrosis (*V. anguillarum*) in eels exposed to copper (Rødsaether et al. 1977) and in epizootics of *Aeromonas liquefaciens* (= *A. hydrophila*) in salmon and suckers exposed to copper and zinc pollution (Pippy and Hare 1969), although in

[16]Stevens, D. G. 1977. Survival and immune response of coho salmon exposed to copper. Environ. Prot. Agency - 600/3-77-031, 37 p.

neither instance were antibody titers determined. In the latter instance, *A. liquefaciens* is an ubiquitous water bacterium, but only causes disease and mortalities in fish with lowered resistance (Snieszko 1962).

Reduction in antibody response to injected virus was demonstrated by Perlmutter et al. (1973) in blue gourami, *Trichogaster trichopterus*, to result from overcrowding. The authors postulated that stressed fish released a pheromonelike immunosuppressive factor under crowded conditions. It is reasonable to expect that other types of environmental stresses could result in a similar response.

Among the invertebrates, indirect evidence for reduction of disease resistance caused by contaminant exposure is available and has already been discussed in previous sections on crustacean shell disease and shrimp virus disease. Direct experimental evidence however, is scarce. Fries and Tripp (1976) exposed hard (hard-shell) clams to phenol and found damage to gill and digestive tract epithelia—tissues which are considered important components of internal defense mechanisms. The authors suggested, but did not demonstrate, that phenol-treated clams may be more susceptible to microbial infections than normal ones. In other studies with invertebrates, Telford (1968, 1974) demonstrated that environmental stress affected blood glucose levels in *Homarus americanus* and crayfish, *Cambarus clarkii*.

POLLUTANT-PARASITE INTERACTIONS

Much has been said and much documentation exists about the role of environmental stress in induction, severity, and persistence of disease. Some of the best information about stress and disease in fish comes from studies concerned with aquaculture—where environmental factors such as temperature, oxygen, water quality, salinity, and diets clearly influence the course of disease and the impact of disease on cultured populations.

There is also a developing body of information, from experimental work as well as from field observations and surveys, about the possible relationship of parasitism and pollution. The relationship is not simple, and in essence involves a double-edged phenomenon, in which pollutant stress may result in an increase (or in some instances decrease) in the prevalence of certain parasites, or in which parasitization may decrease host resistance to toxic pollutants. Subsidiary issues quickly emerge however, such as the effects of pollutants on intermediate or alternate hosts in parasite life cycles, possible effects of pollutants on free-living life cycle stages of parasites, and effects of pollutants on host defenses against parasite invasion.

Thus far in this review, the role of microbial infectious agents, principally viruses and bacteria, has been emphasized, but there is some limited evidence that environmental pollution may change the relationships among animal parasites and their fish hosts (Esch et al. 1975).

Looking first at the influence of parasites on host susceptibility to contaminants, several recent papers (principally from studies in freshwater) offer significant insights. Boyce and Yamada (1977) found in laboratory experiments that sockeye salmon, *Oncorhynchus nerka*, smolts with preexisting parasitization by the intestinal pseudophyllidean cestode *Eubothrium salvelini* were more susceptible to zinc poisoning than unparasitized siblings. Similarly, Pascoe and Cram (1977) found that survival times of the threespine stickleback, *Gasterosteus aculeatus*, exposed to various concentrations of cadmium, were much shortened if the fish were parasitized by the larval cestode *Schistocephalus solidus*. Perevozchenko and Davydov (1974) found that juvenile carp parasitized by the intestinal cestode *Bothriocephalus gowkongensis* were more susceptible to DDT poisoning than were nonparasitized individuals. These results are not surprising, since fish already weakened by parasites would undoubtedly be less able to tolerate other environmental stresses. The nature and degree of parasitization of fish clearly must be considered in bioassays and in studies of effects of contaminants on fish and shellfish species.

Looking next at the reverse viewpoint, the influence of contaminants on parasite prevalence, definitive information is less readily available for marine species, but some information is available for freshwater species. Thermal loading was associated with changes in the distribution and abundance of two larval trematodes in mosquitofish (Aho et al. 1976). Similarly, thermal loading from a nuclear power plant was directly correlated with incidence of the ciliate *Epistylis* sp. and the bacterium *Aeromonas liquefaciens* (= *A. hydrophila*) in six species of centrarchids in South Carolina (Esch et al. 1976). Effects of ther-

mal effluents on parasitism of largemouth bass, *Micropterus salmoides*, by the acanthocephalan *Neoechinorhynchus cylindratus* were examined by Eure and Esch (1974). Parasite densities were significantly higher in fish from heated water during the winter months, a possible reflection of greater densities of larval parasites and intermediate host populations in the effluent. River pollution from domestic and industrial sources was considered to be a contributing factor in increased parasite burdens found in fish from areas of heaviest pollution in Poland (Dabrowska 1974).

For marine species, good evidence relating pollutants with changes in parasite abundance is scarce. Results of an extensive survey of external parasites and disease conditions in North Sea fish (Möller[17]) did not disclose clear-cut relationships between parasitism and pollution, although the higher prevalence of vibriosis and lymphocystis in southern sectors which are most polluted indicated a possible influence of pollution. Other factors seemed responsible for differential abundances reported for the larger external parasites.

Several parasites of estuarine fishes from the Gulf of Mexico were examined by Overstreet and Howse (1977) in a search for associations with environmental pollution. Samples of Atlantic croaker were collected in 1970-72, and again in 1975. Large variations in prevalences of helminth parasites occurred, but clear associations with pollutants and changes in pollutant levels were not established. A myxosporidan protozoan seemed to be more promising. Infections of sheepshead minnows by *Myxobolus lintoni* were very abundant in one polluted bayou of Mississippi, but were absent in seemingly healthy habitats.

The stalked peritrich ciliate *Epistylis* sp., mentioned in an earlier section in connection with fin erosion and red sores, seems to be related to high organic content and possibly other stresses in freshwater and brackish water habitats. The ciliate, together with secondary bacterial invaders (principally *Aeromonas liquifaciens* (= *A. hydrophila*), produces a hemorrhagic hyperplastic condition beneath the scales that is referred to as red sore (Overstreet and Howse 1977). The ciliate infests a wide range of fish species in low salinity waters of Mississippi, especially centrarchids, sheepshead, and black drum (the drum is a marine invader in brackish water). Secondary bacterial infections associated with the ciliate may become systemic, and mortalities may result.

In addition to field observations, there is some experimental evidence for a causal relationship between specific pollutant chemicals and fungus parasitization of fish and shellfish. In one study, oysters exposed to pesticides (DDT, Toxaphene, and parathion) became infected with a mycelial fungus that caused lysis of the mantle, gut, gonads, gills, visceral ganglion, and kidney tubules (Lowe et al. 1971). None of the control oysters became infected, indicating a role for one or several of the pesticides in altering the host-parasite relationships of the oysters and the fungus. Presence of fungus infections made it difficult to differentiate histopathological effects of pesticide exposure from those due to the parasite.

CONCLUSIONS

In considering pollution-associated diseases of fish and shellfish, a number of conclusions seem warranted:

1. Environmental stress from pollutants seems to be an important determining factor in several fish and shellfish diseases. Effects include direct chemical-physical damage to cell membranes or tissues, modification of physiological and biochemical reactions, increased infection pressure from facultative microbial pathogens, and reduced resistance to infection.
2. The multifactorial genesis of disease in marine species is becoming apparent, involving environmental stress, facultative pathogens, resistance of hosts, and latent infections.
3. Some circumstantial evidence for the role of environmental carcinogens in the etiology of neoplasms of fish and shellfish is accumulating, but at present definitive conclusions are not justified.
4. The presence of marginal or degraded estuarine/coastal environments may be signalled by the appearance of, or the increase in prevalence of a number of diseases, including fin erosion, "red sores," ulcers, and possibly lymphocystis in fish; by "shell disease" in crustaceans; and by certain neoplasms in bivalve molluscs, but an absolute cause and

[17]Möller, H. 1977. Distribution of some parasites and diseases of fishes from the North Sea in February, 1977. Int. Counc. Explor. Sea, Fish. Improv. Comm., Doc. CM1977/E:20, 16 p.

effect relationship has not yet been demonstrated for most of these diseases.

5. Among the most severe and persistent problems in establishing pollutant-disease relationships are: the absence of baseline information about the organisms and their habitats prior to pollution, the existence of multiple pollutants in many badly degraded waters, and the circumstantial nature of much of the evidence linking pollution and disease.
6. A number of viruses have been found in crustaceans and molluscs in recent years, and the pathogenic role of two of them (shrimp *Baculovirus* and oyster *Herpesvirus*) has been demonstrated by exposure to increasing environmental stress. Other latent virus infections of invertebrates may be identified by similar experimental methods.

The evidence for an association of pollution and disease presented in this paper (except for results of experimental studies) is largely circumstantial. When confronted with the hard question "Can you state positively that the disease condition seen in natural populations is caused by specific environmental contaminants?", the answer at present has to be "No." However, the weight of this circumstantial evidence, particularly for diseases such as fin erosion and ulcers, is such that it leads to the conclusion that associations do exist between pollutants and disease.

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VERTICAL DISTRIBUTION, DIEL VERTICAL MIGRATION, AND ABUNDANCE OF SOME MESOPELAGIC FISHES IN THE EASTERN SUBARCTIC PACIFIC OCEAN IN SUMMER[1]

BRUCE W. FROST AND LAWRENCE E. MCCRONE[2]

ABSTRACT

Vertical distributions of myctophid fishes and other components of the mesopelagic micronekton were determined during the summers of 1973-75 at two stations in the eastern subarctic Pacific Ocean. Stratified samples were collected with a multiple net Tucker trawl so that the entire water column extending to between 385 and 460 m could be sampled during a daytime or nighttime period; two to four day and night vertical series of samples were obtained each summer. Four species of myctophids made up 87% of the total fish catch: *Stenobrachius leucopsarus* and *Diaphus theta*, which performed diel vertical migrations of 300 m vertical extent; and *Protomyctophum thompsoni* and *S. nannochir*, which exhibited only slight diel variation in vertical distribution. Populations of each myctophid species tended to be vertically stratified by age or size with larger individuals occurring in samples taken progressively deeper. Two other major components of the micronekton were euphausiids and decapod shrimps, chiefly *Euphausia pacifica* and *Sergestes similis*; both species were conspicuous diel vertical migrators. Samples collected in horizontal hauls immediately following sunset showed that three migratory species, the two migratory myctophids and *E. pacifica*, were closely associated with the single migratory sound-scattering layer (12 kHz); *S. similis* lagged the ascent of the migratory scattering layer. A single, deep, nonmigratory sound-scattering layer corresponded closely to the distribution of *P. thompsoni* during both day and night. As in other subpolar oceanic waters, abundance and standing stock of myctophids were high—0.9 fish/m² and 0.37 g dry weight/m².

In 1973 we began a field study of some small mesopelagic fishes of the family Myctophidae, commonly known as lanternfishes or myctophids, in the eastern subarctic Pacific Ocean. The objectives of the study were to determine the vertical distribution and migration characteristics of the numerically dominant species, to document their feeding behavior, and to ascertain if the distributions of fish were in any way influenced by the distribution of their preferred prey. Myctophids are major components of the mesopelagic fauna throughout the world ocean, and in most areas they are sufficiently abundant and stratified in the water column to cause deep sound-scattering layers (Baird et al. 1974; McCartney 1976). Indeed, study of these fishes has been heavily oriented toward aspects of their distribution in relation to sound-scattering layers (e.g., Tucker 1951; Barham 1966; Taylor 1968; Holton 1969; Farquhar 1971; Baird et al. 1974), although some investigations emphasized aspects of biological and ecological significance, such as individual growth rates, seasonal changes in abundance, and association among species (e.g., Pearcy and Laurs 1966; Harrisson 1967; Lavenberg and Ebeling 1967; Smoker and Pearcy 1970; Badcock 1970; Clarke 1973; Pearcy et al. 1977). Much of the research on myctophids has, in addition, stressed description of the prominent diel vertical migrations which are apparently undertaken by almost all species.

In the few species studied in detail, both the occurrence and pattern of vertical migration vary with age or ontogeny. Larval myctophids are nonmigratory, spending day and night in near-surface waters (Ahlstrom 1959). Diel vertical migration is first evident at or shortly after metamorphosis and usually persists throughout the remaining life of the fish, although in very old fish, migrations may differ substantially in character from those of younger fish and may even be supressed (Nafpaktitis 1968). Apart from this variation with age, diel vertical migrations of myctophids seem to be relatively regular, on a day-to-day basis, and exhibit little or no seasonal variation (Pearcy and Laurs 1966; Halliday 1970; Pearcy et al. 1977). Among some species, however,

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there may be a portion of the population which does not migrate, while other members of similar size and age do migrate (Clarke 1973; Badcock and Merrett 1976; Pearcy et al. 1977).

Virtually nothing is known about the biological causes or consequences of these diel vertical migrations, either with respect to the myctophids or their environment. Marshall (1954) suggested that myctophids migrate into the surface layer each night in order to feed on zooplankton, which is usually most abundant in surface waters (Vinogradov 1968). As pointed out above, larval myctophids spend both day and night in the zooplankton-rich surface layer, but as the larvae grow they perhaps become more conspicuous to visual predators and, after metamorphosis, they descend to greater depths,returning to the surface layer only at night, if at all. Vertical migrations may indeed have evolved as a means of avoiding or minimizing predation, but it is unlikely that this hypothesis can be tested in the ocean.

On the other hand, it is practicable to investigate the feeding ecology of myctophid fish in relation to their migrations; for example, what types of prey the fish utilize, when and where in the water column the fish feed, and whether the vertical distributions of the fish are affected by the vertical distribution and abundance of their preferred prey. As necessary background for such a study, in this paper we present details of the vertical distributions of the numerically dominant species of myctophids in the eastern subarctic Pacific Ocean.

METHODS

Study Area

We conducted the investigation during three summer cruises in areas centered at lat. 50°N, long. 145°W (July-August 1973 and July-August 1975; Station P in Figure 1) and at lat. 51°N, long. 137°W (July 1974; Station Q in Figure 1). These stations lie within the hydrographic province designated the Central Subarctic Domain by Dodimead et al. (1963). We chose the subarctic region for ease of sampling and identifying the fish and zooplankton. For example, in an earlier meridional cruise from Kodiak, Alaska, to Honolulu, Hawaii (August-September 1972), we found that deep sound-scattering layers are fewer in number, shallower, and more intense in the subarctic region than in transition and subtropical waters (Frost unpubl. data). Apparently related to this, the subarctic myctophid fauna is a simple one; only a few species are abundant, and they are relatively shallowly distributed in the daytime (Taylor 1968). Further, the study area is an open ocean environment, outside the potentially complicating influences of coastal and transitional waters (cf. McGowan 1971) and is roughly in the middle of the latitudinal range of several species of myctophids. Finally, the zooplankton assemblage in subarctic waters is also less diverse than in lower latitudes, it is well known taxonomically, and relatively few species are abundant.

FIGURE 1.—Sampling stations in the eastern subarctic Pacific Ocean. Representative hydrographic domains for summer conditions after Dodimead et al. (1963).

Sampling Gear

Nekton samples were collected with a modified Tucker trawl (Tucker 1951) described by Frost and McCrone (1974). Briefly, the trawl had a rigid rectangular mouth with a 4-m^2 area when inclined forward at a 45° angle from vertical, and carried five separate nets (6.35-mm stretch mesh, knotless nylon ace netting) stacked one on top of another (much like fig. 4 in Harding et al. 1971). The net shape followed the design of Clarke (1969). The trawl carried an electronics package containing a strain gage pressure transducer (range 0-1,500 lb/in^2) for determination of depth and a precision pendulum-type tilt transducer (range 0°-90° from vertical) for determination of angle of inclination of the trawl mouth. A TSK (Tsurumi-Seiki Kosakusho)[3] flowmeter fitted with a magnetic

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

reed switch was mounted on the top beam of the trawl.

The trawl was towed on a two-conductor coaxial cable and its depth, angle of inclination of the mouth, and revolutions of the flowmeter were monitored continuously during trawling by means of a shipboard display unit. The nets were opened and closed at the mouth by means of a net-tripping assembly which was controlled electronically from the ship. The bottom net (without cod end) was left open during deployment to eliminate kiting of the trawl when a net was first opened (Clarke 1969; Badcock and Merrett 1976); thus, four sequential samples could be collected in one haul. The volume of water filtered by each net (assuming 100% filtration efficiency) was calculated from flowmeter revolutions and average angle of inclination of the net mouth.

To determine vertical distributions of fish and other components of the nekton, we towed the trawl obliquely and collected samples on the upward leg of a haul. We monitored the speed of the ship during trawling by reference to a Doppler ship's speed indicator.

Recordings of deep sound-scattering layers were obtained using an Edo-Western transducer operating at 12 kHz (pulse length 3-10 ms, beam width about 33°) and a Precision Depth Recorder (PDR) operating on the 0-400 fm (0-732 m) depth range scale. At the beginning of each cruise, echosounder characteristics (pulse length, power output) and recorder gain were set to give optimal resolution of the sound-scattering layer and were not varied thereafter.

Sampling Program

Taylor (1968) found a close correlation between distribution of abundant species of myctophid fishes and distribution of deep sound-scattering layers in the eastern subarctic Pacific near the Queen Charlotte Islands. Relying on this correlation, at each station we designed our sampling program after observing the depth and migrations of deep sound-scattering layers. The number, depth, and migration of scattering layers were virtually identical at Stations P and Q. We observed no differences between years at Station P, and our observations do not differ substantially from those of Bary (1967) who also used a 12-kHz echosounder in summer at Station P. In the daytime, a single, diffuse, sound-scattering layer extended from about 275 to 375 m depth (Figure 2A). In the late afternoon and early evening, this scattering layer became broader, chiefly by upward movement of the top of the layer, and it persisted with relatively little further change throughout the night. At about 2130 h (local time), a single, upwardly migrating layer became evident, and within half an hour it merged completely with the surface reverberation (Figure 2B). This migratory scattering layer began descent at about 0530 h and merged with the deep nonmigratory layer shortly after 0600 h. Slight variations in times of ascent

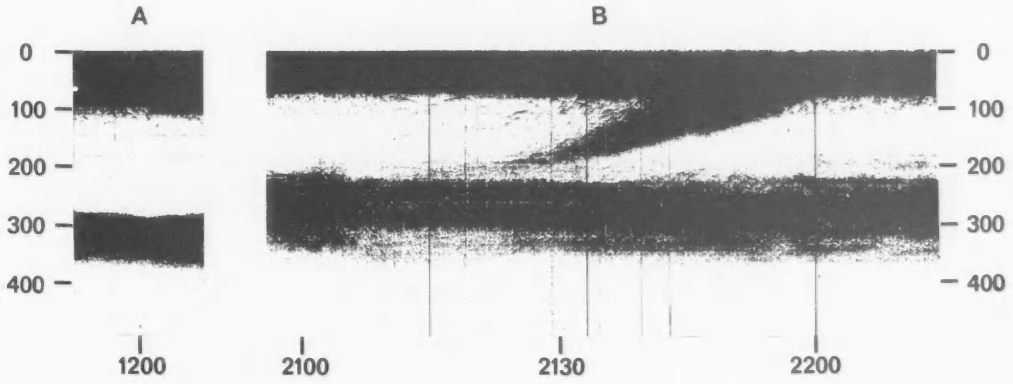

FIGURE 2.—12-kHz echograms typical of the summer period (July-August) in the sampling areas in the northeastern Pacific Ocean. A. Daytime record about noon, local time. B. Evening record taken on the same day showing the upward movement of the migratory sound-scattering layer and the persistence of the nonmigratory layer at depth. Local time, depth in meters. The dark areas above 100 m are due to surface reverberation.

and descent of the migratory sound-scattering layer depended on weather conditions; also, year-to-year differences are attributed to slight variations in time of cruises. We usually set the lower limit of nekton sampling at least 50 m below the depth of the deep nonmigratory scattering layer. With the exceptions noted below, nighttime sampling was confined to the time period between ascent and descent of the migratory scattering layer.

Somewhat different sampling programs were carried out in different years (Table 1). At Station P in 1973 the objective was to obtain information on vertical distributions of fish and zooplankton to aid in developing an optimal sampling strategy for studying diet and feeding behavior of myctophids. The 0-440 m water column was sampled in 55-m depth strata, and seven successive vertical series of samples, 4 night and 3 day series, were obtained. A shallow haul (0-220 m) and a deep haul (220-440 m) were required for each complete vertical series. The first nighttime series was not completed before the descent of the migratory sound-scattering layer. In order to obtain both the shallow and deep hauls during one night, the hauls were of relatively short duration, and consequently the nekton samples were relatively small.

At Station Q in 1974, the objectives were to confirm the vertical distributions found in 1973 at Station P and to document the feeding chronology of the common myctophids. The sampling for vertical distributions (Table 1) extended from the surface to between 400 and 460 m, depending on the depth of the deep sound-scattering layer, and usually included one sample collected below the scattering layer. Complete daytime vertical series (both shallow and deep hauls) of samples were collected on 2 days; as no fish were collected in the upper 200 m, two additional daytime vertical series were made with only one haul extending from below the depth of the sound-scattering layer to about 200 m. In order to achieve adequate sample size, the duration of each haul was long, but because there were so few hours of darkness, only one nekton haul could be made each night. Data from a shallow haul and a deep haul on successive nights were therefore combined to give a single, complete, night vertical series; two such night series were obtained, and all sampling was performed between ascent and descent of the migratory sound-scattering layer.

In addition to vertical series of nekton samples taken at Station Q, we utilized two types of horizontal hauls. To identify components closely associated with the migratory sound-scattering layer, on two evenings the trawl was launched near sunset and towed horizontally at 125 m. The 12-kHz echosounder was operated continuously during the hauls. Approximately 30 min before the scattering layer began to ascend from its daytime depth, a trawl net was opened and sampling began. The second net was opened just as the scattering layer reached 125 m, and the net was closed after the layer had passed that depth. The trawl was towed at 125 m for an additional 30 min, taking a third sample, then closed and retrieved. As part of the study of diel variations in feeding intensity of myctophids, a series of three horizontal hauls, each yielding four samples of 30 min duration, was made in the upper layer (40-m depth) throughout one night.

The sampling program at Station P in 1975 was similar to that at Station Q, although the nekton sampling for vertical distributions (Table 1) was much less extensive than in the previous two cruises. We obtained only one complete nighttime vertical series (400-0 m) and two deep daytime vertical series (385-220 m) to check on vertical distributions of myctophids. We collected one shallow vertical series in the 0-60 m layer in 15-m depth strata to examine the vertical distribution of myctophids within the surface layer at night, and we took one very deep daytime vertical series (782-440 m) to determine the distribution of myctophids below our usual sampling depths.

All samples obtained with the nekton trawl were preserved in a 4% formaldehyde seawater solution buffered with sodium borate.

TABLE 1.—Sampling data for vertical series of nekton samples in the northeastern Pacific. The three lower entries for Station P (1975) represent data for: first, the routine day-night vertical series (0-400 m); second, a single shallow (0-60 m) night vertical series; and, third, a single deep (440-782 m) daytime vertical series.

Stn.	Dates	Ship speed (km/h)	Mean (range) duration of samples (min)	Mean (range) volume filtered per sample (m^3)	
P	5-9 Aug. 1973	7.2±0.5	29 (16-45)	8,412	(4,863-13,357)
Q	18-22 July 1974	6.2±0.5	45 (24-66)	14,229	(6,833-20,361)
P	26-28 July 1975	6.9±0.5	32 (19-43)	10,984	(7,664-14,731)
	27 July 1975	6.9±0.5	21 (16-29)	7,638	(6,184-10,052)
	31 July 1975	6.9±0.5	68 (58-79)	23,232	(20,012-28,614)

Analysis of Samples

All organisms in the nekton samples were counted. Fish were identified from descriptions in Hart (1973) and Wisner (1976). The standard length (SL) (distance from the tip of the snout to the end of the vertebral column) of each fish was measured to the nearest millimeter. Among the invertebrates collected in nekton samples, only euphausiids and decapod shrimps were consistently captured in substantial numbers. The numbers of fish and shrimp were standardized to number per 10,000 m^3 of water.

Myctophid fish, preserved for about 3 yr, were sorted from samples for determination of body length and dry body weight. Intact, undamaged specimens were dried to constant weight at 65°C on glass slides in a drying oven. Drying usually took 3-4 days, but up to 10 days for some of the largest fish. Dried fish were weighed to the nearest milligram. The relationship between standard body length and dry body weight for each species of myctophid was determined by linear regression analysis of logarithmically transformed measurements.

RESULTS

The vertical series of nekton samples collected at Stations P and Q yielded nine species of myctophids, one abundant species of chauliodontid, and one relatively rare melanostomiatid. All other families combined made up only 2-6% of the total catch by number (Table 2). In addition to fish, the samples contained considerable numbers of euphausiids and decapod shrimps. Other invertebrate groups, such as siphonophores and squids, were only sporadically captured. The more common fishes had similar relative abundances at the two stations. More than 80% of the myctophids consisted of three species (*Stenobrachius leucopsarus*, *Protomyctophum thompsoni*, and *Diaphus theta*) whose vertical distributions were generally well bracketed by the sampling. The other species of myctophids were either rare or appeared to be distributed below the usual range of sampling; therefore, emphasis in this study was placed on the above three, abundant, relatively shallowly distributed species.

Vertical Distribution of Fish

The most abundant fish in our samples was *S. leucopsarus*. Its only congener, *S. nannochir*, was rarer (Table 2). As discussed later, with the exception of the very deep vertical series (782-440 m) in 1975, only small specimens (<35 mm) of *S. nannochir* occurred in the vertical series. The fish caught at Station P in 1973 were in such poor condition that it was not possible to discriminate the smaller specimens of the two species of *Stenobrachius*. However, there is evidence (presented below) that *S. nannochir* was extremely rare at Station P in 1973, much rarer than at Station Q or Station P in 1975 (Table 2). Redesign of the cod ends, after the 1973 cruise, provided us with good specimens which permitted discrimination of the two congeners.

TABLE 2.—Composition of the total fish catch in vertical series of nekton samples in the northeastern Pacific. Data for each station combine all vertical series.

Family and species	Station P, 1973		Station Q, 1974		Station P, 1975	
	No.	%	No.	%	No.	%
Myctophidae:						
Stenobrachius leucopsarus	720	63.8	1,038	45.4	461	49.3
S. nannochir	([1])	([1])	268	11.7	92	9.8
Protomyctophum thompsoni	125	11.1	413	18.1	210	22.5
Diaphus theta	111	9.8	304	13.3	61	6.5
Tarletonbeania crenularis	16	1.4	26	1.1	3	0.3
Lampanyctus regalis	9	0.8	11	0.5	0	0
L. ritteri	3	0.3	11	0.5	0	0
Notoscopelus japonicus	1	0.1	0	0	0	0
Symbolophorus californiense	1	0.1	0	0	0	0
Chauliodontidae:						
Chauliodus macouni	57	5.0	147	6.4	84	9.0
Melanostomiatidae:						
Tactostoma macropus	21	1.9	15	0.7	3	0.3
Others	64	5.7	55	2.4	21	2.2
Totals	1,129		2,288		935	

[1]Due to the poor condition of the fish caught at Station P in 1973, it was impossible to discriminate the smaller specimens of the two species of *Stenobrachius*. It is possible that some of the fish listed here as *S. leucopsarus* were in fact *S. nannochir*, but for reasons described in the text, we do not believe this to be the case.

At Station P in 1973, *S. leucopsarus* occurred in largest numbers in the surface layer (0-55 m) at night and at 275-330 m during the day (Figure 3A). This pattern could occur if most specimens undertook a diel vertical migration over a depth range of 250-300 m. To be certain that the data reflect a vertical migration and not simply light-aided avoidance of the net by fish in the daytime, it was necessary to compare day and night total catches of fish integrated over the water column sampled (Table 3). Assuming that the entire vertical range of *S. leucopsarus* was sampled (this assumption is qualified below), then it is clear that, since the total catches for day and night series were statistically indistinguishable (Table 3), there was no evidence of daytime avoidance of the trawl by fish. Further, judging from the results of replicate sampling of zooplankton with nets (Wiebe and Holland 1968), the day and night totals in Table 3 are well within the range of variability expected for repeated samples from a pelagic population. Thus, the observed diel differ-

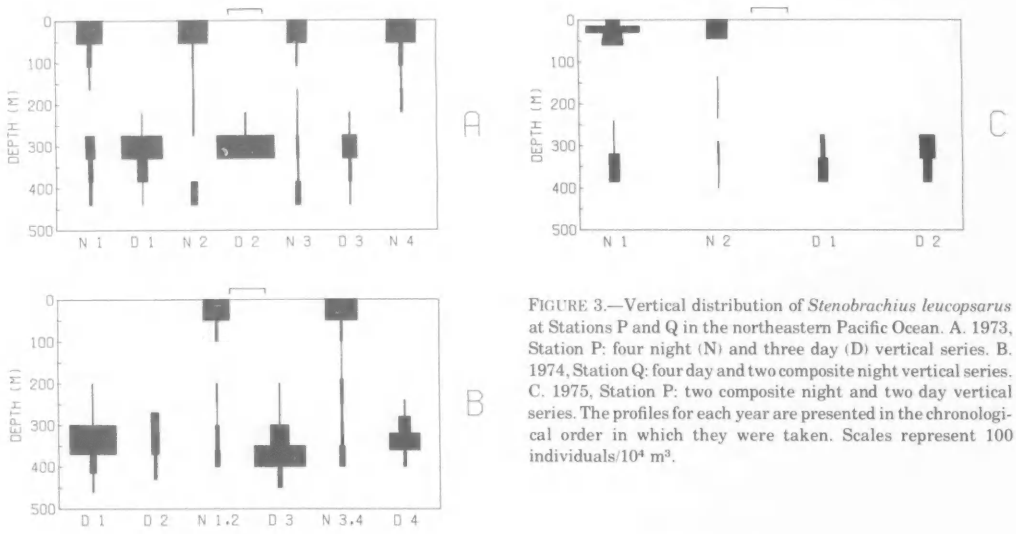

FIGURE 3.—Vertical distribution of *Stenobrachius leucopsarus* at Stations P and Q in the northeastern Pacific Ocean. A. 1973, Station P: four night (N) and three day (D) vertical series. B. 1974, Station Q: four day and two composite night vertical series. C. 1975, Station P: two composite night and two day vertical series. The profiles for each year are presented in the chronological order in which they were taken. Scales represent 100 individuals/10^4 m^3.

TABLE 3.—Day and night total catches for the water column sampled, of selected fish and crustacean species at Stations P and Q in the northeastern Pacific; means and ranges (parentheses) as number/100 m^2. Ratios given of largest to smallest estimate of abundance for a station.

Species	Station	Day		Night		Ratio
Stenobrachius leucopsarus	P, 1973	67.7	(28.6-82.0)	59.8	(47.3-73.7)	2.9
	Q, 1974	101.1	(48.4-153.6)	62.1	(56.5-67.7)	3.2
	P, 1975	28.0	(20.3-35.8)	37.6	(29.2-46.1)	2.3
Diaphus theta	P, 1973	6.8	(1.1-13.8)	12.4	(3.9-18.2)	16.5
	Q, 1974	22.6	(15.2-34.4)	[1]11.5	(11.0-12.0)	3.1
	P, 1975	3.6	(3.1-4.0)	5.4	(3.6-10.4)	3.4
Protomyctophum thompsoni	P, 1973	15.6	(12.7-20.9)	7.9	(0.0-13.8)	[2]4.8
	Q, 1974	26.7	(21.6-39.1)	23.6	(20.0-27.3)	2.0
	P, 1975	17.3	(17.2-17.3)	47.0	(28.9-65.2)	3.8
Chauliodus macouni	Q, 1974	10.1	(3.2-15.7)	8.2	(7.5-9.0)	4.9
Euphausia pacifica	P, 1973	169.7	(24.2-323.9)	[1]1,075.3	(214.5-5,825.0)	240.7
	Q, 1974	417.4	(272.0-531.5)	154.0	(17.5-290.5)	30.4
	P, 1975	322.5	(223.8-421.3)	423.7	(294.5-532.9)	2.5
Sergestes similis	P, 1973	19.8	(0.5-31.3)	[1]50.3	(28.0-80.8)	161.6
	Q, 1974	33.0	(14.0-47.6)	[1]72.9	(57.5-88.3)	6.3
	P, 1975	10.2	(9.3-11.0)	11.1	(9.6-12.6)	1.4

[1]Day and night abundance significantly different ($P < 0.1$) by rank test (Tate and Clelland 1957).
[2]Estimate based on smallest nonzero catch.

ences in the vertical distribution of *S. leucopsarus* (Figure 3A) indicate that the majority of individuals do perform a diel vertical migration.

The occurrence of some *S. leucopsarus* in the deepest samples at night (Figure 3A) indicates that the entire population was not participating in the vertical migration described above. Differences in migratory pattern appear to be largely a function of size or age of individual fish. The length-frequency histogram for our entire catch of *S. leucopsarus* at Station P in 1973 (Figure 4A) indicates that several size classes of fish were sampled. Since *S. leucopsarus* metamorphoses to the juvenile stage at 18 mm (Smoker and Pearcy 1970), the abundant 19-35 mm size class (Figure 4A) probably represented the youngest juvenile fish. The largest specimens caught at Station P attain the maximum size expected for *S. leucopsarus*, 85-111 mm (Kulikova 1957; Smoker and Pearcy 1970).

To determine the effect of size on vertical migration, we examined the three obvious size classes of *S. leucopsarus*: 19-35 mm, 38-82 mm, and 90-112 mm. The smallest size class (19-35 mm) performed a clear diel vertical migration from 275-330 m in the daytime to 0-55 m at night (Figure 5A). The anomalously low density of fish on the third day must be attributed to horizontal patchiness of fish. Note especially that only on one night (N3, Figure 5A) was one small-sized *Stenobrachius* captured below 275 m. The medium size class (38-82 mm) shows a similar migration (Figure 5B), though these fish seemed to be more dispersed vertically, both at night and in the daytime, than the smallest size class. The high density of medium-sized fish at 275-330 m on the first night, not apparent on the other three nights, probably reflected the fact that this sample was collected between 0554 and 0613 h, a time period when the migratory sonic scatterers, and presumably myctophids, were descending. Some of the medium-sized fish probably had already descended into the 275-330 m layer at the time this sample was collected. The largest size class of *S. leucopsarus* (90-112 mm) had a pattern of vertical distribution totally different from those of the two smaller size classes. Individuals of the largest size class were not captured at all in the first two daytime series and were caught only in the two deepest samples in the third daytime series (Figure 5C). They were captured in all four night series, but never in the surface layer (0-55 m), and in three of the four night series, the greatest density of large-sized fish occurred between 330 and 440 m. It is tempting to conclude from these data that the individuals of the largest size class also perform a diel vertical migration, moving from daytime depths below our lower limit of sampling (440 m) into our sampling range at night. Of course, a similar vertical distribution pattern could be obtained if the largest fish avoid the trawl in the daytime, although it seems unlikely that all fish of this size class could effectively do so. Nevertheless, with the data from Station P (1973), it is impossible to discriminate between these two possibilities for the largest fish.

Stenobrachius leucopsarus had a very similar pattern of distribution and diel vertical migration at Station Q (Figure 3B). The length-frequency distribution of the species was strongly skewed to juvenile fish (19-31 mm), which made up 88.7% of the total catch of the species. There was only one relatively distinct secondary mode, consisting of very large fish (81-108 mm), which composed 3.9% of the total catch (Figure 4B). Fish in the smallest mode and also the rarer intermediate sizes of fish (32-79 mm) were clear vertical migrants, closely following the pattern described above for Station P, and there was no difference in vertical distribution between the small- and medium-sized fish. Also, as at Station P, representatives of the largest size class of fish were captured, with the exception of 1 fish (out of 45 caught) in the deepest sample on day 4, only in the night hauls and almost always (43 out of 44 fish) below 50 m.

At Station P in 1975, the same patterns of diel vertical migration (Figure 3C) and size-dependent variation in vertical distribution of *S. leucopsarus* were evident, though far fewer fish were collected, both because of the fewer vertical series taken and an apparent decrease in abundance of the species compared with the previous 2 yr (Table 3). This decrease appears due partly to reduced abundance of the smallest size class (17-32 mm) which made up only 47.2% of the total catch in 1975 (Figure 4C), compared with 62.6% at Station P in 1973 and 88.7% at Station Q. In the one deep daytime vertical series (782-440 mm) at Station P, large *S. leucopsarus* were captured between 440 and 740 m (Table 4), thus supporting our earlier hypothesis that the largest fish caught at night above 440 m migrated in the daytime below our usual range of sampling. However, extensive day and night sampling over the entire vertical range of the large fish is required to completely rule out daytime avoidance of the trawl.

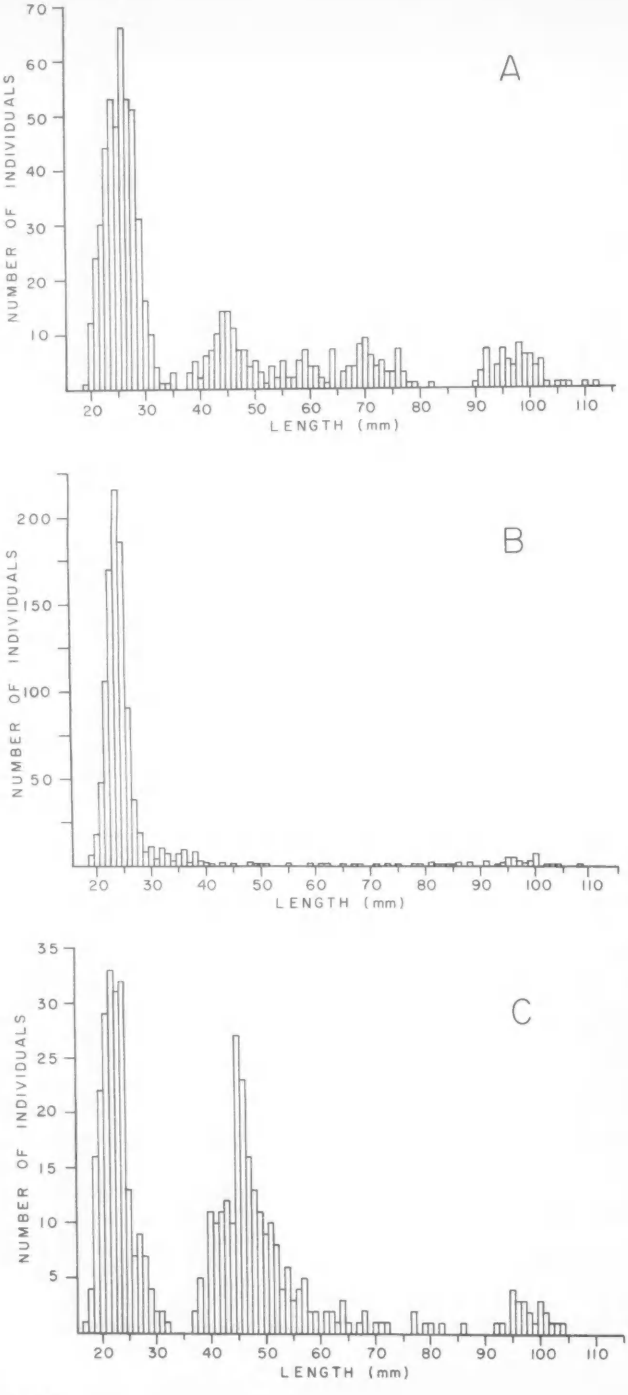

FIGURE 4.—Length-frequency distributions of *Stenobrachius leucopsarus* from all vertical series. A. 1973, Station P, N = 720. B. 1974, Station Q, N = 1,038. C. 1975, Station P, N = 461.

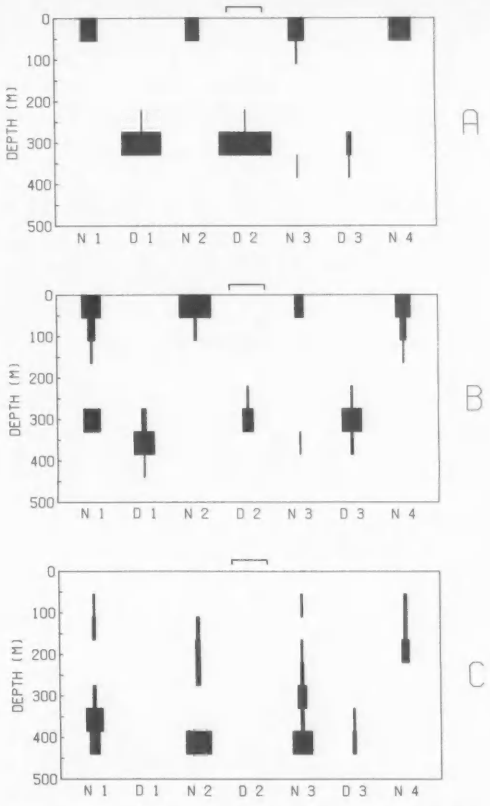

FIGURE 5.—Vertical distribution of three sizes of *Stenobrachius leucopsarus* at Station P, 1973. A. 19-35 mm, scale represents 100 individuals/10^4 m^3. B. 38-82 mm, scale represents 50 individuals/10^4 m^3. C. 90-112 mm, scale represents 25 individuals/10^4 m^3. Sequence of vertical series as in Figure 3A.

The one shallow night vertical series (60-0 m) at Station P indicated that *S. leucopsarus* were distributed throughout the surface layer but were concentrated between 15 and 30 m (Figure 3C). Examination of sizes of fish caught in this series suggested very fine-scale vertical stratification by age or size (Table 5). Recall that in all other vertical series taken at night very large fish (>80 mm) were always captured (except for one fish) below 50 m. Because we took only one such shallow vertical series, we cannot evaluate the frequency of occurrence or temporal persistence of this apparent stratification of fish by age in the surface layer at night.

The third most abundant myctophid in our samples, *Diaphus theta*, also performed a diel vertical migration (Figure 6); there was no consistent difference between day and night catches (Table 3). At night, *D. theta* ranged over the upper 165 m but was concentrated near the surface (0-55 m), while during the day most of these fish were collected below 275 m. As stated above for *S. leucopsarus*, the occurrence of *D. theta* at 275-330 m the first night at Station P (1973) is misleading because the sample was probably collected after the downward vertical migration of myctophids had begun.

The size range for the total catch of *D. theta* was 36-88 mm in 1973 and 46-84 mm in 1975 at Station P, and 33-76 mm at Station Q. The size-frequency distributions were similar in all 3 yr. Considering only Station Q, for which we have the largest collection, the size-frequency distribution (Figure 7A) was quite different from *S. leucopsarus* (Figure 4B). Small and large fish were rare and the samples contained primarily intermediate sizes (45-58 mm). Distinguishing, somewhat arbitrarily, three classes in the size-frequency distribution, there is indication of size-dependent

TABLE 5.—Vertical distribution of size classes of *Stenobrachius leucopsarus* in the shallow night vertical series at Station P (1975) in the northeastern Pacific, as number/10,000 m^3. Data based on a single haul with a single sample at each depth.

Depth (m)	17-32 mm	37-82 mm	>85 mm
0-15	37.2	1.6	0
15-30	140.5	13.6	0
30-45	7.8	46.8	0
45-60	15.9	42.8	1.0
Total no. captured	138	89	1

TABLE 4.—Deep daytime vertical distribution of selected species of micronekton at Station P (1975) in the northeastern Pacific, as number/10,000 m^3. For *Stenobrachius leucopsarus*, the numbers in parentheses are abundances of large fish (91-112 mm SL). Data based on a single haul with a single sample at each depth.

Depth (m)	*Stenobrachius leucopsarus*	*Stenobrachius nannochir*	*Protomyctophum thompsoni*	*Lampanyctus ritteri*	*Chauliodus macouni*	*Sergestes similis*
440-540	4.5 (3.5)	49.6	0.7	0	2.4	10.8
540-640	8.5 (7.5)	7.0	0	0	0	7.5
640-740	4.4 (1.3)	4.9	0	0.9	0.4	0
740-782	0	2.7	0.5	0.5	0	0
Total no. captured	40 (28)	173	3	3	8	45

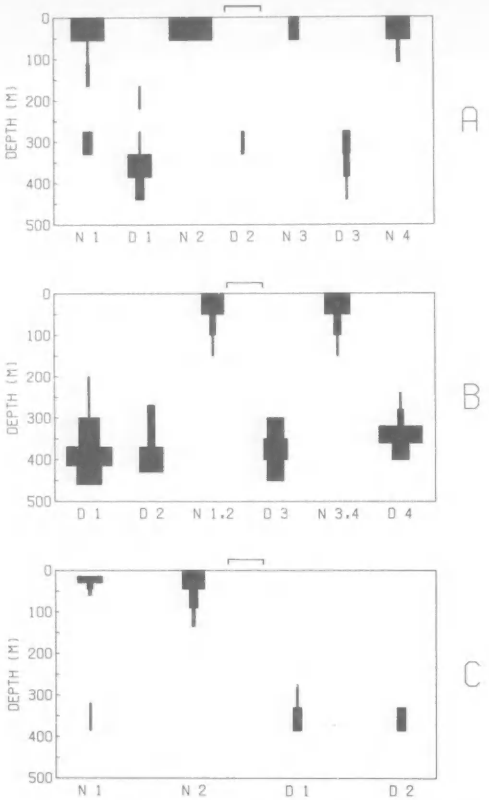

FIGURE 6.—Vertical distribution of *Diaphus theta*. A. 1973, Station P. B. 1974, Station Q. C. 1975, Station P. Scales represent 25 individuals/10^4 m^3. Sequence of vertical series as in Figure 3.

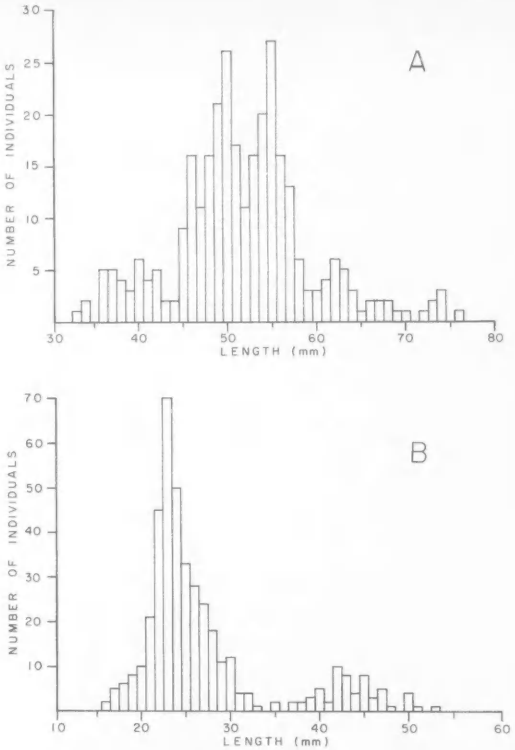

FIGURE 7.—Length-frequency distributions of *Diaphus theta* (A), $N = 304$, and *Protomyctophum thompsoni* (B), $N = 413$, from all vertical series at Station Q, 1974.

variation in vertical distribution and vertical migration. The smallest sizes (35-44 mm) of fish were consistently shallower than larger sizes both during the day and at night (Table 6); although the numbers of fish are small, they do indicate a possible trend. *Diaphus theta* was not captured in the very deep (782-440 m) daytime vertical series at Station P in 1975.

The second most abundant myctophid, *Protomyctophum thompsoni*, did not perform an extensive diel vertical migration similar to that of *S. leucopsarus* or *D. theta*; it remained below about 200 m both day and night (Figure 8). Nevertheless, the species tended to be somewhat more shallowly distributed at night than in the daytime. This is best demonstrated by the data from Station Q where the largest catches of this species were made. At Station Q, *P. thompsoni* ranged from 16 to 53 mm SL and the length-frequency distribution of the population was bimodal (Figure 7B). Calculations of mean depths of the two size classes showed that the smaller fish were always slightly more shallowly distributed that the larger fish (Table 6). Moreover, both size classes tended to be deeper in the daytime than at night, although the average change in depth (30-40 m for both size classes) was relatively small (Table 6). *Protomyctophum thompsoni* was rare below 440 m at Station P in 1975 (Table 4). The size range of the species at Station P was 18-51 mm (1973) and 16-50 mm (1975), and the size-frequency distribution was similar to that of Station Q.

The above three species of myctophids had vertical distributions which were, with the possible exception of the rare large specimens of *S. leucopsarus*, well bracketed by our vertical series of samples. Two other relatively abundant species of fish seemed to have vertical distributions which

TABLE 6.—Mean depth (meters) of size classes of *Diaphus theta* and *Protomyctophum thompsoni* in day (D1-D4) and night (N1, N2) vertical series at Station Q in the northeastern Pacific. Mean depth D was calculated from the equation $D = \Sigma n_i \bar{Z}_i / \Sigma n_i$, where n_i is the population density (number/10,000 m³) of a size class in sample i and $\bar{Z}_i$ is the midpoint of the depth range of sample i.

Size class (mm)	D1	D2	D3	D4	N1	N2	Total no. captured
Diaphus theta:							
35-44	342	357	325	336	25	25	40
45-58	394	382	377	351	32	30	224
>58	390	400	404	344	76	69	40
Protomyctophum thompsoni:							
16-35	332	316	330	301	294	257	354
36-53	381	338	340	340	307	309	59

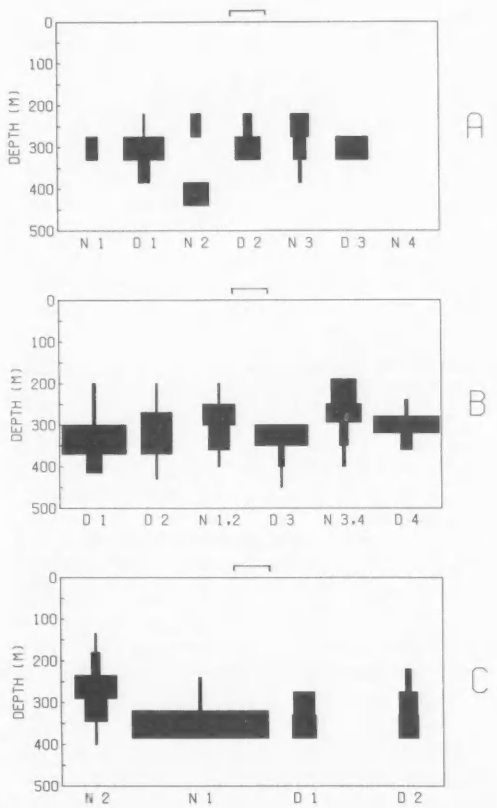

FIGURE 8.—Vertical distribution of *Protomyctophum thompsoni*. A. 1973, Station P. B. 1974, Station Q. C. 1975, Station P. Scales represent 25 individuals/10^4 m³. Sequence of vertical series as in Figure 3.

extended deeper than our usual range of sampling. *Stenobrachius nannochir* was only captured below 275 m in the routine vertical series at Stations Q (1974) and P (1975). As noted earlier, due to the poor condition of the catch, small specimens of *S. nannochir* and *S. leucopsarus* were not distinguished in samples from Station P (1973). Half of the total catch of *S. nannochir* was from below 400 m, and all of the specimens caught above 440 m were <35 mm SL. It is for this reason that we think that the species must have been extremely rare in the 0-440 m layer at Station P in 1973, for we caught almost no small *Stenobrachius* in the deep samples at night (Figure 5A). The virtual restriction of catches of *S. nannochir* to our deepest samples, day and night, indicates that its distribution probably extended below our range of sampling. Indeed, it was the most abundant fish in the one very deep daytime vertical series at Station P (1975); it occurred down to 782 m and was concentrated in the 440-540 m layer (Table 4). Furthermore, an interesting vertical stratification by size was evident in this series, with the smallest fish dominating the shallowest sample and largest fish dominating the deepest two samples (Table 7). Note that we captured only small specimens (<35 mm) in all of the other, shallower vertical series. *Stenobrachius leucopsarus* and *S. nannochir* of similar body size tended to be vertically well separated in the water column at all times (Tables 4, 7; Figure 5).

TABLE 7.—Vertical distribution of size classes of *Stenobrachius nannochir* in the deep daytime vertical series at Station P (1975) in the northeastern Pacific, as number/10,000 m³.

Depth (m)	22-37 mm	38-70 mm	85-113 mm
440-540	37.0	12.2	0.3
540-640	0.5	6.5	0
640-740	0	2.2	2.7
740-782	0	0.9	1.8
Total no. captured	107	55	11

The only other moderately abundant fish was the chauliodontid *Chauliodus macouni*, and only at Station Q was it captured in sufficient numbers to warrant description. *Chauliodus macouni* always occurred below 150 m, and there was no conclusive evidence of change in its vertical distribution during the day-night cycle (Figure 9, Table 3). However, in contrast to *P. thompsoni*, whose range of vertical distribution apparently was well sampled day and night (Figure 8B, Table 4), it appears from the abrupt truncation of histograms in Figure 9 that the deepest portion of the population of *C. macouni* was not sampled either in the daytime or at night. Indeed, in the very deep vertical series at Station P (1975), a number of *C. macouni* were captured in the 440-540 m layer

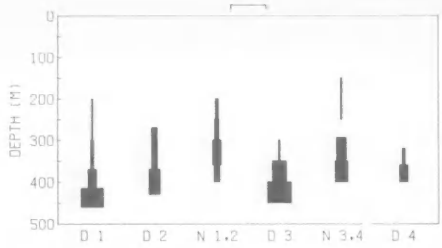

FIGURE 9.—Vertical distribution of *Chauliodus macouni* at Station Q, 1974. Scale represents 25 individuals/10^4 m^3. Sequence of vertical series as in Figure 3B.

TABLE 8.—Abundance (number/10,000 m^3) of *Stenobrachius leucopsarus* and *Diaphus theta* in three series of half-hour samples collected in horizontal tows at 40-m depth during one night at Station Q in the northeastern Pacific. Sampling commenced after the migratory scattering layer had merged with the surface reverberation and terminated after the scattering layer had descended below the surface reverberation (0425). Time is when net was opened.

Time	*S. leucopsarus*	*D. theta*	Time	*S. leucopsarus*	*D. theta*
2200	157	31	0130	262	42
2230	89	15	0200	329	36
2300	102	10	0300	188	72
2330	109	8	0330	178	66
0030	80	21	0400	146	28
0100	197	54	0430	8	0

(Table 4), indicating that the distribution of this fish probably extended below the normal limit of sampling in the routine vertical series. At Station Q, specimens of *C. macouni* ranged from 29 to 189 mm SL. Very large fish (>100 mm) were usually captured at night in the deepest samples, but for fish <100 mm there was no clear trend of size-dependent variation in vertical distribution.

Other fish species (Table 2) occurred sporadically in the samples and were caught primarily at night: the only daytime catches were below 300 m (e.g., *Lampanyctus ritteri* in Table 4). Included in the category "Others" in Table 2 were members of the families Bathylagidae, Gonostomatidae, Melamphaeidae, Opisthoproctidae, Paralepididae, and Scopelarchidae.

Variability in Abundance of Myctophids in Replicated Samples

With a few exceptions, the estimates of abundance of myctophids integrated over the water column sampled did not vary by more than a factor of 4 between vertical series within cruises (Table 3). At Station Q, three series of half-hour horizontal hauls were made at 40 m throughout one night (Table 8). Excluding the sample (0430) collected after the scattering layer had descended, concentrations of *S. leucopsarus* varied by a factor of about 4, those for *D. theta* by a factor of about 9. For both species, there was a significant trend ($P = 0.05$, run test, Tate and Clelland 1957) toward increased abundance during the night, and their abundances were strongly correlated (rank difference correlation coefficient 0.74, $P \sim 0.01$, Tate and Clelland 1957). Myctophids were abundant in the surface layer until the migratory scattering layer descended.

Estimated Abundance and Standing Stock of Fishes

Our data for mean abundance of all fishes captured for the 3 yr ranged from 0.78 to 1.61/m^2 for the water column extending to between 385 and 460 m (Table 9). The three most abundant species of myctophids combined accounted for 77-85% by number of all fish collected. There was no consistent difference between day and night estimates of concentrations of fish.

Equations for the regression of dry body weight on body length (Table 10) were used in conjunction with the lengths and abundance of fish from each sample to calculate the population standing stocks of *S. leucopsarus*, *D. theta*, and *P. thompsoni* for

TABLE 9.—Estimated mean abundance and standing stock of mesopelagic fishes at Stations P and Q in the eastern subarctic Pacific Ocean. Myctophids includes only the three most abundant species, *Stenobrachius leucopsarus*, *Diaphus theta*, and *Protomyctophum thompsoni*. Estimated mean abundance and standing stock are based on average of all day and night vertical series; values in parentheses are means for night vertical series only.

Station	Abundance (no./m^2)		Standing stock (g dry wt/m^2)
	Myctophids	All fishes	Myctophids
P, 1973	0.85	1.00	0.53 (0.77)
Q, 1974	1.24	1.61	0.27 (0.39)
P, 1975	0.61	0.78	0.34 (0.55)

TABLE 10.—Equations for the regression of dry body weight, W (grams), on body length, L (centimeters), for three species of myctophids.

Species	Regression equation	Range of SL (cm)	N
Stenobrachius leucopsarus	$W = 0.00125\ L^{3.546}$	2.0-11.8	92
Diaphus theta	$W = 0.00537\ L^{2.943}$	3.0-7.4	79
Protomyctophum thompsoni	$W = 0.00212\ L^{3.391}$	1.7-4.9	54

each vertical series of nekton samples at each station. A slight (<1%) bias toward underestimation of weight was corrected using the approximation for minimum variance unbiased estimator of the mean given by Beauchamp and Olson (1973). Mean standing stock, averaged over day and night series, ranged from 0.27 to 0.53 g dry weight/m² of sea surface (Table 9). Variations in standing stock did not closely follow variations in abundance because of large year-to-year variations in the size-frequency distribution of the most abundant species, *S. leucopsarus* (cf. Figure 4). For example, the low standing stock at Station Q is due to the relative scarcity of medium-sized (40-80 mm) *S. leucopsarus* in the catch at that station (Figure 4B). This also accounts for differences between years in the composition by species of the standing stock of the three myctophids. At Station P in both years, *S. leucopsarus* represented, on the average, 63.4-75.7% of the standing stock of myctophids, but at Station Q it contributed only an average of 32.4%. At Station Q, the rarer, but relatively larger, *D. theta* made up 59.3% of the standing stock; however, at Station P it made up only 21.2-24.3%. *Protomyctophum thompsoni*, because of its small body size (Figure 7B), averaged <13% of the standing stock at all stations (range of means for the three stations, 4.2-12.3%). Estimates of mean standing stock based only on night vertical series tended to average more than those based only on day series (Table 9) because of the contribution from the relatively rare (Figure 5), but very large (>90 mm), specimens of *S. leucopsarus* which were caught chiefly at night.

Vertical Distribution of Crustaceans

The most abundant organisms in the vertical series of nekton samples were euphausiids, predominantly large individuals (>12 mm total length). At Station P in both 1973 and 1975, *Euphausia pacifica* made up more than 80% of the euphausiid catch by number. At Station Q, 51% of the total euphausiid catch was *E. pacifica*; other species were *Thysanoessa spinifera* (30%), *Tessarabrachion occulatum* (9%), *Thysanoessa longipes* (8%), and *Stylocheiron maximum* (2%). All of these species also occurred at Station P, but were rare. Consequently, only the data for *E. pacifica* are presented here.

During the day, large *E. pacifica* occurred in greatest concentration between 275 and 400 m, while at night they were usually concentrated in the upper 55 or 60 m (Figure 10). No consistent difference between day and night total catches was evident, but sporadic, extraordinarily large or small catches of *E. pacifica* were obtained in both 1973 and 1974. Variations such as these are common in euphausiid catches (Brinton 1962b) and are usually attributed to horizontal patchiness. Our ranges of estimated abundances were consequently very large (Table 3). The other four species of euphausiids were too rare to draw definite conclusions about their distributions.

The penaeid decapod shrimp, *Sergestes similis*, was the only other abundant invertebrate in our nekton samples. At Station P (1973) and Station

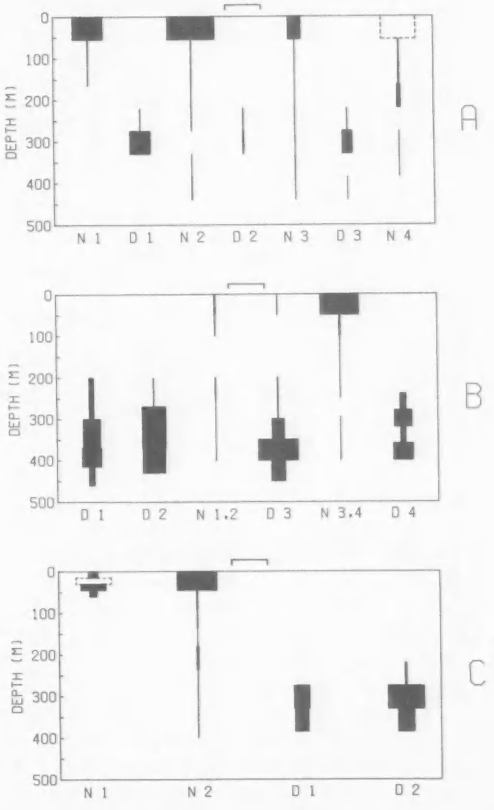

FIGURE 10.—Vertical distribution of *Euphausia pacifica*. A. 1973, Station P. Scale represents 1,000 individuals/10⁴ m³. (The 0-55 m sample on the fourth night represents 10,447 individuals/10⁴ m³.) B. 1974, Station Q. Scale represents 500 individuals/10⁴ m³. C. 1975, Station P. Scale represents 500 individuals/10⁴ m³. (The 15-30 m sample on the first night represents 3,086 individuals/10⁴ m³.) Sequence of vertical series as in Figure 3.

Q, the species appeared to be performing an extensive diel vertical migration (Figure 11A, B); however, the average daytime catches at both stations were a bit less than half the average nighttime catches, though only in 1973 and 1974 were there statistically significant differences (Table 3). Except for the largest size class of *Stenobrachius leucopsarus* (Figure 5C), *Sergestes similis* is the only species for which we found such a prominent, repeated, day-night difference in catches. Either *S. similis* is a diel vertical migrator and descends below our usual range of sampling in the daytime or it is capable of avoiding the nekton trawl in the daytime. Our very deep daytime vertical series taken at Station P (1975) bears on this question. Although the species seemed considerably less abundant in 1975 (Table 3), this was probably partly due to the shallower depth to which the routine vertical series extended in the daytime. In the very deep daytime vertical series, *S. similis* occurred in considerable numbers between 440 and 640 m (Table 4). Thus it probably was a migrator and in the daytime ranged well below the greatest depth of sampling on routine vertical series.

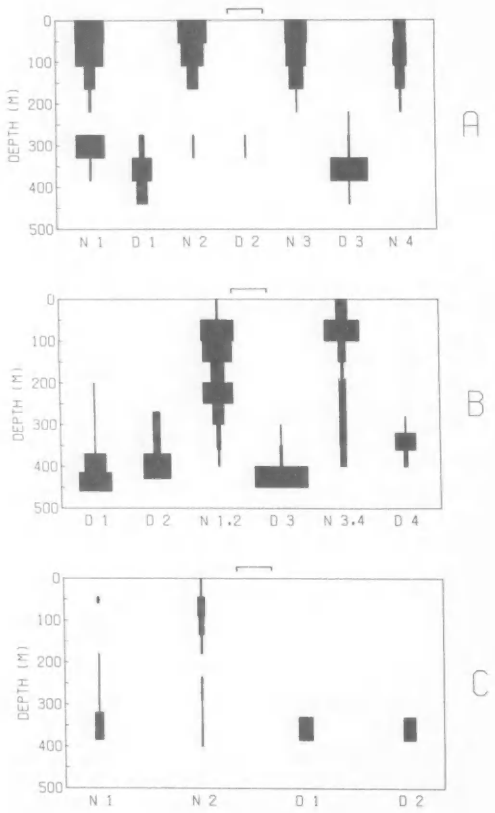

FIGURE 11.—Vertical distribution of *Sergestes similis*. A. 1973, Station P. B. 1974, Station Q. C. 1975, Station P. Scales represent 50 individuals/10^4 m^3. Sequence of vertical series as in Figure 3.

At both stations, *S. similis* tended to be rather broadly distributed over the 0-150 m layer at night and often was more abundant below 50 m than above (Figure 11). In this respect its diel migration differs from that of the two migratory myctophid fishes and *E. pacifica*, which tended to aggregate strongly above about 60 m at night.

In addition to *S. similis* several other types of malacostracans were collected in the samples: the caridean decapods *Hymenodora frontalis*, *Notostomus japonicus*, and *Pasiphaea* sp.; the penaeid decapod *Bentheogennema borealis*; and the mysids *Gnathophausia gigas*, *Boreomysis* sp., and *Eucopia* sp. All were rare, were collected only at night, and almost always occurred below 200 m.

Micronekton Associated With Sound-Scattering Layers

In the daytime, the position of the scattering layer corresponded closely with the daytime depth of occurrence of the smaller size classes of *Stenobrachius leucopsarus* and the populations of *D. theta* and *Protomyctophum thompsoni* (Figure 12A). For example, in the profiles shown in Figure 12A, the 300-400 m stratum contained an average concentration of 136 fish/10,000 m^3 of the three species combined. *Sergestes similis* is distributed too broadly and deeply in the daytime to contribute to the observed scattering layer (Figure 11B, Day 3). Excluding euphausiids, in our samples no other potential sound-scattering organism (e.g., physonect siphonophores) consistently had its center of abundance between 275 and 400 m in the daytime. The large *E. pacifica* collected with the nekton trawl had a pattern of vertical distribution (Figure 10B, Day 3) very similar to that of the migratory myctophid fishes.

Comparison of the vertical distribution and diel migration of *Stenobrachius leucopsarus* with the echosounder trace indicates a correlation between the fish and the migratory sound-scattering layer (Figures 2, 3). The correlation is best for individuals of the small and medium size classes (Figure 5). Similarly, the vertical distribution and diel mi-

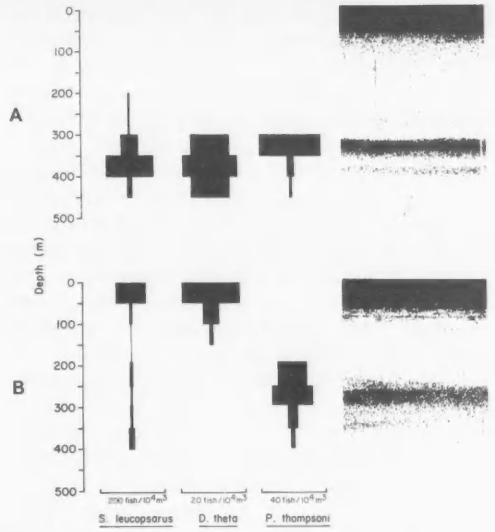

FIGURE 12.—Vertical distribution of three species of myctophids relative to a sound-scattering layer recorded with the 12-kHz echosounder. A. Midday distribution of fish and an echogram showing the position of the scattering layer at the time of sampling (Day 3 at Station Q). B. Nighttime distribution of fish and an echogram showing the position of the scattering layer at the time of sampling (Nights 3, 4 at Station Q).

gration of *D. theta* closely parallel the behavior of the migratory sound-scattering layer (Figures 2, 6). To examine this relationship more closely, at Station Q two series of three horizontal samples each were collected at 125 m in the periods preceding, during, and after ascent of the migratory sound-scattering layer past that depth. In the first series (Table 11, 17 July) both *S. leucopsarus* and *D. theta* were most abundant in the sample collected as the scattering layer was passing 125 m. Euphausiids (predominantly *E. pacifica*) and *Sergestes similis* were also abundant in the samples; however, maximum concentrations of each were obtained either in the sample collected before or after the scattering layer had passed 125 m (Table 11). Results from the second series (Table 11, 18 July) were similar except that euphausiids were not as abundant in the first sample of the series, and *Stenobrachius leucopsarus* was most abundant in the sample collected after the scattering layer had passed 125 m. The results, therefore, indicate that both migratory myctophids and euphausiids are associated with the migratory sound-scattering layer, whereas sergestid shrimps are not.

TABLE 11.—Occurrence of migratory myctophids and crustaceans (number/10,000 m³) in two series of three samples collected in horizontal hauls at 125 m depth before, during, and after ascent of the migratory sound-scattering layer past that depth.

Species	17 July			18 July		
	Before	During	After	Before	During	After
Stenobrachius leucopsarus	0	38	1	0	13	27
Diaphus theta	1	37	5	0	25	0
Euphausia pacifica	87	64	1	5	68	2
Sergestes similis	3	13	53	0	4	82

Position of the nonmigratory portion of the deep sound-scattering layer which was present at night was strongly correlated with the distribution of *P. thompsoni*, particularly the small size class. The scattering layer was broader and more diffuse at night, and so was the distribution of *P. thompsoni* (Figures 2, 8, 12B). Over the 200-300 m stratum, the average concentration of *P. thompsoni* was 16.3 fish/10,000 m³ for the profile shown in Figure 12B. The day-to-night persistence of the nonmigratory scattering layer (Figure 2) cannot be explained by reference to the distribution of either *S. leucopsarus* or *D. theta*. The two smaller size classes of *S. leucopsarus* and all *D. theta* have migrated into the surface layers at night, and the largest *S. leucopsarus* are not only rare but broadly distributed over 50-450 m. There are no other abundant potential sound-scattering organisms concentrated in the 200-300 m stratum at night.

DISCUSSION

Previous work on myctophids in open waters of the subarctic Pacific dealt chiefly with systematics and biogeography (Wisner 1976). However, Aron (1962) and Taylor (1968) considered aspects of the distribution of myctophids in eastern subarctic waters. Aron's (1962) results are qualitative due to the nature of the sampling gear used (unmetered, nonclosing nets of variable mesh size). Differences between results of our study and those of Taylor's (1968) comprehensive investigation are probably attributable to the different sampling gear employed rather than to fundamental variations in behavior of fish in different parts of the subarctic Pacific. For example, Taylor's use of very course-meshed nets probably accounts for both his finding of different relative abundances of myctophid species and for somewhat different patterns

of vertical distribution of species. Thus in Taylor's study, carried out not far from Station Q, *P. thompsoni* and *D. theta* were more abundant than *S. leucopsarus*, but this was probably because Taylor's net either did not efficiently catch juvenile (<35 mm) *S. leucopsarus* which were the numerically dominant size class of that species in our samples (Figure 4), or they were much less abundant during the time he sampled. Further, Taylor obtained some of the largest catches of *D. theta* and *S. leucopsarus* below 90 m at night. This probably also reflects the sampling bias of his net for larger sizes of fish, which at night tend to be more broadly spread over the water column than smaller fish (Figure 5C; Table 6, night series). Unfortunately, Taylor did not report the sizes of fish captured. Except for probable sampling bias toward larger sizes of fish, Taylor's results on vertical distribution of the nonmigratory *P. thompsoni* and other species of fish agree with ours.

Pearcy et al. (1977) described patterns of vertical distribution of mesopelagic fishes and crustaceans off the coast of Oregon. The mesopelagic assemblage there is essentially subarctic in faunistic affinity and the vertical distributions of species are similar to those observed at Stations P and Q. The only notable departure from our results was the finding by Pearcy et al. that significant numbers of all sizes of *S. leucopsarus* did not participate, at least on a regular basis, in the diel vertical migrations. Our observations at both Stations P and Q indicate that virtually all *S. leucopsarus* smaller than about 80 mm performed extensive diel vertical migrations (Figure 5). However, in our studies, *S. leucopsarus* was also very rare below 400 m (Figure 5, Table 4), whereas Pearcy et al. found large concentrations below that depth. Thus there may be major differences in the vertical distribution and migration behavior of *S. leucopsarus* in different parts of its geographical range (Paxton 1967). Significantly, Pearcy et al. (1977) detected no seasonal variations in vertical distributions and migrations for any species, which may also be true for subarctic waters to the north (Taylor 1968).

Perhaps the most remarkable feature of the mesopelagic fauna of the area sampled was its simplicity. Only four species of myctophid fishes were abundant in the upper 700 m. Two of these species, *S. leucopsarus* and *D. theta*, undertook diel migrations of substantial vertical extent; the other two, *P. thompsoni* and *S. nannochir*, did not. Other taxonomic groups also showed low diversity. Among the micronektonic crustaceans there were single species of abundant euphausiid, *E. pacifica*, and decapod shrimp, *Sergestes similis*, and both were vertical migrators. The contrast between this relatively simple mesopelagic micronekton fauna and that, for example, in the subtropical North Pacific (Brinton 1962a; Clarke 1973; Walters 1977) or subtropical North Atlantic (Badcock 1970; Foxton 1970a, b) is striking, but not atypical. Low taxonomic diversity of the mesopelagic micronekton is found in other subpolar oceans, such as the Boreal Atlantic (e.g., Backus et al. 1971; Zahuranec and Pugh 1971).

Associated with the taxonomic simplicity of the mesopelagic fauna herein reported, was a relatively simple structure of the sound-scattering layers. Generally, both the number and depth of sound-scattering layers change with latitude in the deep ocean; fewer and shallower layers are found in subpolar oceans than in tropical-subtropical oceans (Haigh 1971; Cole et al. 1971; Donaldson and Pearcy 1972; Tont 1976). Our unpublished observations on deep sound-scattering layers (12-kHz echosounder), taken in September 1972 along long. 155°W between Alaska and Hawaii, showed this trend. Subarctic waters had the relatively simple sound-scattering structure illustrated in Figure 2, with single migratory and nonmigratory layers occurring shallower than 400 m. In the subtropical waters near Hawaii, at least three sound-scattering layers were observed in the daytime at depths ranging from 260 to 625 m, and three to four migratory layers were recorded.

It is unlikely that the correlation between taxonomic diversity of the mesopelagic micronekton and complexity of the sound-scattering structure in the water column was fortuitous. Attempts to causally relate deep sound-scattering layers to aggregations of mesopelagic organisms were stimulated by hypotheses advanced more than three decades ago (for a review see Hersey and Backus 1962). However, field studies based on net samples taken simultaneously with echosounder records tend to be inconclusive for a variety of reasons. A major difficulty is that different taxonomic groups tend to occur together at the same depths and may even show similar migratory behavior. For example, all four of the migratory mesopelagic species in our study (*Stenobrachius leucopsarus*, *D. theta*, *E. pacifica*, and *Sergestes similis*) ascended towards the surface layer after

sunset, and only from fine temporal spacing of samples did it become apparent that some species were more closely associated with the scattering layer than others (Table 11). Similarly, in the daytime some of these migratory species cooccurred at the depth of the sound-scattering layer together with the nonmigratory *P. thompsoni*, and any or all could have contributed to the daytime sound-scattering layer. Despite extensive cooccurrence of several types of potential sound-scattering organisms, the most reasonable hypothesis is that myctophids were primarily responsible for both the migratory and nonmigratory sound-scattering layers in the eastern subarctic Pacific.

Taylor (1968), also working in the subarctic Pacific, found the best correlation between deep sound-scattering layers and those mesopelagic fish which possessed gas-filled swim bladders. Although Taylor grouped *Stenobrachius leucopsarus* and *D. theta* among fish with fat-invested swim bladders, gas is present in the swim bladders of immature individuals (<30 mm SL) of both species (Capen 1967). Taylor made no mention of the size of the fish caught in his study; however, in view of the very coarse-meshed nets he used, it is probable that he did not quantitatively sample immature fish. At Stations P and Q, some individuals of *S. leucopsarus* and *D. theta* were theoretically the right size to resonate at 12 kHz while at their daytime depths (Capen 1967), and the abundance of either species was probably sufficient to produce deep sound-scattering in the daytime (Hershey and Backus 1962). This presumably holds also for *P. thompsoni*, which has a gas-filled swim bladder throughout life (Taylor 1968; Butler and Pearcy 1972). Indeed, concentrations of either *D. theta* or *P. thompsoni* alone in Figure 12 were comparable with the concentration of *D. taaningi*, which Baird et al. (1974) believe was responsible for the migratory sound-scattering layer over the Cariaco Trench.

As pointed out above, *Sergestes similis* may be excluded as a potential sound scatterer; it was distributed too broadly and deeply in the daytime and lagged the ascent of the migratory sound-scattering layer at sunset (Figure 11, Table 11). Although *E. pacifica* (Figure 10) was about five times more abundant in the depth of the daytime sound-scattering layer than all myctophid fishes combined, it did not approach concentrations necessary for it to be an effective scatterer of 12-kHz sound (Hersey and Backus 1962; Bary 1966; Beamish 1971).

In conclusion, we suggest that the nonmigratory deep sound-scattering layer (Figure 2B) in the vicinities of Stations P and Q in the eastern subarctic North Pacific was caused by *P. thompsoni*, and that the migratory sound-scattering layer (Figure 2B) recorded the migrations of smaller size classes of *Stenobrachius leucopsarus* and *D. theta*. *Protomyctophum thompsoni* may have been largely responsible for the deep scattering layer observed in the daytime, with possible lesser contributions from the two migratory myctophid species. Pearcy (1977) found similar general correspondence between vertical distributions of the same three species of myctophids and deep sound-scattering layers off Oregon, but he pointed out that quantitative correlation between abundance of potential sound-scatterers and distribution of volume scattering was not always strong. A more definitive analysis, similar to that of Baird et al. (1974), is required; that is, simultaneous observations should be obtained on distribution of volume scattering and abundance and acoustical properties of suspected sound-scatterers.

In single hauls, we observed concentrations of myctophids, all species combined, which regularly exceeded 100 fish/10^4 m^3 in the region of the deep sound-scattering layer in the daytime and in the surface layer at night. Similar concentrations of myctophids are found in other oceans (e.g., Kashkin 1967). Further, the maximum concentrations of myctophids observed by us in the surface layer at night (365 fish/10^4 m^3, Table 8) and at depth in the daytime (874 fish/10^4 m^3, horizontal haul at 327-333 m, Station Q) equal or exceed maximum concentrations inferred from the apparently high catch rates of single hauls reported by Halliday (1970) and Backus et al. (1971) for the western Boreal Atlantic, where one species of myctophid, *Benthosema glaciale*, predominates. The very low concentrations of myctophids found by Pearcy et al. (1977), using a 2.4 m Isaacs-Kidd midwater trawl, are puzzling and seem to indicate that myctophids are about 1/10 as abundant off the Oregon coast as in the open subarctic Pacific. However, the data of Pearcy et al. (1977) differ from the earlier results of Pearcy and Laurs (1966), in which reported concentrations of myctophids were much higher and similar to concentrations observed by us; the difference could be due to year-to-year variability (Pearcy 1977).

There is relatively little variability between years in our estimates of abundance of myctophid fishes (the three most abundant species, Table 2)

in the water column extending to 385-460 m. We estimate 0.61-1.24 myctophid fish/m² based on averaged day and night series (Table 10). No quantitative study comparable to ours has been made in the open subarctic Pacific, but Pearcy and Laurs (1966) provided data on the abundance of mesopelagic fish near the Oregon coast. In two cruises (August 1963), Pearcy and Laurs found about 0.78 myctophid fish/m² in the 0-500 m water column at night; this estimate is based upon the three numerically dominant myctophid fish captured (Pearcy and Laurs 1966, fig. 4), two of which ranked 1 and 3 in abundance among myctophids in our study. The average standing stock of all mesopelagic fish found by Pearcy and Laurs (1966) was 2.9 g wet weight/m² in the 0-500 m water column at night. Using a factor of 0.3 to convert wet weight to dry weight, the average nighttime standing stock is 0.87 g/m², a value probably not significantly different from our estimates based on night samples (Table 9), especially since the Pearcy and Laurs estimate is based on all mesopelagic fish captured. Similar concentrations of myctophids (about 0.6-0.8 fish/m²) are found in the subtropical Pacific near Hawaii (Clarke 1973; Maynard et al. 1975). However, many more species of myctophids (47) occur there, and the standing stock of myctophids (about 0.3-0.7 g wet weight/m²) is somewhat less than our estimates (0.23-0.53 g dry weight/m², Table 9), probably because the fish are considerably smaller in average size (Clarke 1973).

With regard to sampling bias, we found no evidence of light-aided avoidance of the nekton trawl by either myctophids or other types of micronekton occurring in the upper 385-460 m during the daytime (Table 3). Consistent day-night differences in catches of organisms, such as those observed for the largest size class (>80 mm SL) of *S. leucopsarus* and for *Sergestes similis*, were probably due to migration of these organisms below the depth range of daytime sampling. The results of the single very deep vertical series at Station P (Table 4) support this interpretation. Furthermore, very deep vertical migrations of both species are well documented in other parts of their geographical ranges in the North Pacific (Omori et al. 1972; Pearcy et al. 1977).

In addition to determining vertical distributions and vertical migrations of myctophid fishes, on each cruise we also sampled zooplankton with a smaller trawl (Frost and McCrone 1974). Analyses of the zooplankton samples, together with data on stomach contents of the three most abundant myctophids, are the subject of a report (in preparation) on the feeding behavior of myctophids in relation to their vertical distribution and the vertical distribution of their zooplankton prey.

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ANALYSIS OF A SIMPLE MODEL FOR ESTIMATING HISTORICAL POPULATION SIZES

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ABSTRACT

Estimates of historical abundance of animal populations are important in many management decisions. Historical estimates based on a simple model of population growth have been made for several populations of dolphin involved with the yellowfin tuna purse seine fishery. We used the data for the bridled dolphin, *Stenella attenuata*, to investigate the behavior of the model by which these historical estimates were calculated. For populations with low net reproductive rates, the effect of bias in the estimates of the input parameters on the estimated historical abundances was approximately linear and additive. When all the input parameters were independently estimated, the variances of the historical abundance estimates were dominated by the variance of the initial abundance estimate and the coefficient of variation of the historical estimate was less than the largest coefficient of variation of any parameter.

Many decisions about the management of animal populations are based on the estimates of abundance of the population relative to its historical or preexploitation size. These estimates are basic to any application of the theory of maximum sustained yield as incorporated in several international marine mammal management agreements such as the North Pacific Fur Seal Treaty and the International Whaling Convention. Similarly, the concept of "optimum sustainable populations" as specified in the recent Marine Mammal Protection Act of 1972 (MMPA) has been defined in terms of comparing the present size of a population with its original size (Southwest Fisheries Center[3]). Schools of dolphin of several species (primarily *Stenella attenuata* and *S. longirostris*) have been used by purse seine fishermen in the eastern tropical Pacific to locate yellowfin tuna, *Thunnus albacares*, since 1959, as described by Perrin (1969). Significant numbers of dolphin have been killed by becoming entangled in the purse seines. In order to make management decisions under the MMPA about these dolphin populations, the National Marine Fisheries Service (NMFS) needed estimates of the preexploitation abundance of the various populations. The NMFS convened a workshop of scientists to obtain the estimates based on a simple model of population change (see footnote 3). This paper evaluates the behavior of estimates of abundance obtained from their approach. This is important in order to be able to evaluate the degree of confidence to be placed in such estimates, and hence in management plans based on them.

METHODS AND MATERIALS

The model used to estimate preexploitation abundance is based on a common discrete model of population growth:

$$N_{\tau+1} = N_\tau - K_\tau + (N_\tau - K_\tau)(b-d) \qquad (1)$$

where N_τ = the abundance at time τ
b = the birth rate
d = the natural death rate
K_τ = the number of animals killed, assumed to occur at the beginning of time interval τ
$N_{\tau+1}$ = the abundance 1 time unit later.

Reversing the procedure (i.e., solving the above equation for N_τ) results in the expression

$$N_\tau = \frac{N_{\tau+1}}{1+R_\tau} + K_\tau \qquad (2)$$

where N_τ now is the estimate of abundance 1 yr

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earlier and R_τ is the net reproductive rate $(b-d)$. The above model was modified in the procedure used by NMFS to account for situations when the kills occur throughout the time interval instead of instantaneously at the end of the interval, as:

$$N_\tau = \frac{N_{\tau+1}+0.5K_\tau}{1+R_\tau}+0.5K_\tau \, . \qquad (3)$$

This equation can be repeatedly applied to give estimates any number of years (t) into the past. When rearranged to explicitly display the population size t years earlier, and relabeling so that the initial abundance is N_0, one obtains

$$N_t = \frac{N_0}{\prod_{j=1}^{t}(1+R_j)} + \sum_{j=1}^{t} \frac{K_j(1+R_j/2)}{\prod_{i=j}^{t}(1+R_i)} . \qquad (4)$$

Note in this form that the time-index t runs backwards from zero. As is apparent in this form, the estimation of abundance t years earlier involves $2t+1$ parameters. The sequences of annual kills and net reproductive rates can be termed the kill and the net reproductive rate vectors, each composed of t elements.

The data used here to explore this estimation procedure is from the report of NMFS Workshop discussed above (see footnote 3).[4] From existing unpublished data and reports the Workshop participants used estimates of the population size in 1974 and the annual incidental kills and reproductive rates from 1959 to 1974. Several sequences of estimated annual kills and reproductive rates were considered, incorporating the uncertainty in the data.

In the present paper the sequences of annual kills and net reproductive rates given in Table 1 are used to illustrate several general aspects of the behavior of Equation (4). These correspond to the "high kill" and "central reproductive rate" sequences for the bridled dolphin, *Stenella attenuata,* in the Workshop report. The estimate of 1974 abundance used by us and the Workshop was 3.5 million.

[4]It should be noted that the estimates used here are based on a number of assumptions currently under investigation and that these estimates are subject to significant change in the near future (I. Barret, Director, Southwest Fisheries Center, La Jolla, CA 92038, pers. commun. April 1978).

TABLE 1.—Estimates used for kill and reproductive rate vectors of *Stenella attenuata* in the eastern Pacific.

t	Year	Kill (thousands)	Net reproductive rate
1	1973	120	0.040
2	1972	273	.040
3	1971	185	.040
4	1970	308	.036
5	1969	331	.032
6	1968	164	.028
7	1967	194	.024
8	1966	281	.020
9	1965	297	.016
10	1964	255	.012
11	1963	133	.008
12	1962	106	.004
13	1961	446	.000
14	1960	534	.000
15	1959	129	.000

Estimation of Bias

A sensitivity analysis was done to examine the effects of biased parameter estimates on the backcalculated abundance. A new population size 1 yr earlier, from Equation (3), when each parameter is changed by a specified amount is

$$N_1'(n, k, r) = \frac{N_0(1+n)+0.5K_1(1+k)}{1+R_1(1+r)} + 0.5K_1(1+k) \qquad (5)$$

and in general for t years earlier,

$$N_t'(n, k, r) = \frac{N_0(1+n)}{\prod_{j=1}^{t}(1+R_j(1+r))} + \sum_{j=1}^{t} \frac{K_j(1+k)\ (1+(R_j(1+r)/2))}{\sum_{i=j}^{t}(1+R_i(1+r))} \qquad (6)$$

where N_0, R_t, and K_t are defined as above, and

n = the proportion that N_0 deviates from its estimate

r = the proportion that all elements of the net reproductive vector deviate from their estimates

k = the proportion that all elements of the kill vector deviate from their estimates.

$N'_t\,(n,k,r)$ was then compared with N_t from Equation (4) or equivalently $N'_t\,(0,0,0)$. As a measure of the sensitivity of the basic model, $S_t\ (n,k,r)$ is defined to equal the percent that $N'_t\ (n,k,r)$ deviates from N_t

$$S_t(n, k, r) = \left(\frac{N_t(n, k, r) - N_t}{N_t}\right) \cdot 100 . \quad (7)$$

Estimation of Variance

The variance of the backcalculated estimate of N_t from Equation (4) was approximated using the delta method (Seber 1973). This method is based upon a Taylor series expansion for a function in which quadratic and other higher order terms are ignored. If f is a function of the random variables $x_1, x_2, x_3 \ldots, x_n$ then the expression for the variance of f by the delta method is

$$V(f(X_1, X_2, X_3 \ldots, X_n)) = \sum_{i=1}^{n} V(X_i)\left(\frac{\partial f}{\partial X_i}\right)^2 + 2\sum\sum_{i<j} \mathrm{Cov}(X_i, X_j)\left(\frac{\partial f}{\partial X_i} \cdot \frac{\partial f}{\partial X_j}\right) . \quad (8)$$

In applying this expression to Equation (4), it is necessary to be able to define which of the parameters should be considered as random variables, and to give reasonable estimates for value of the variances and covariances of these variables. For the purpose of exploring the behavior of Equation (4), we assumed that the estimates of all the parameters in Equation (4) are independent random variables. The covariance terms in Equation (8) are then zero. This approach provides a picture of the variance of the back estimate of abundance if in fact independent estimates of the kills and the net reproductive rates were available for each year. A generalized expression for the variance using this approach is

$$V(N_t) = V(N_0)\left(\frac{\partial N_i}{\partial N_0}\right)^2 + \sum_{j=1}^{t} V(K_j)\left(\frac{\partial N_i}{\partial N_j}\right)^2 + \sum_{j=1}^{t} V(R_j)\left(\frac{\partial N_j}{\partial R_j}\right)^2 \quad (9)$$

where all parameters are defined as for the basic model [Equation (4)]. For detailed expressions for each of the right hand terms see Appendix I.

As noted the method used for approximating the variance of a function depends on the higher order terms in the Taylor's series expansion being small. The higher order terms in the delta method expression for the variance of N_t are composed of the second and higher order derivatives of N_t with respect to N_0, K_t, and R_t, and the higher order central moments of the probability distributions of the estimates of N_0, K_t, and R_t (i.e., skewness, kurtosis, etc.). The second and higher derivatives with respect to N_t and K_t are zero. Thus the terms involving R_t are the only higher order terms not equal to zero. The higher order derivatives of N_t with respect to R_t involve R_{t+1} to increasing negative powers. The three higher order moments of R_t are always decreasing since R_t is much less than one. Thus each of the higher order terms in the delta method expression for the variance of N_t are each less than the first order term in R_t (iii of Appendix I). The contribution of this first order term in R_t to the variance of N_t is small, as shown below. Thus the error induced by ignoring the higher order terms in the Taylor's series appears small.

The objective in doing the variance calculations was to understand the behavior of the variance of the population size when estimated by the basic back projection model [Equation (4)]. Thus a range of variances was calculated for a range of reasonable values of the variances of the estimated parameters. However, in our example of bridled dolphin estimates of the variance of many of the parameters were not available. Many of the kill estimates were not independently estimated and hence have large unknown covariances (Smith and Polacheck[5]). Estimates of net reproductive rate were obtained by extrapolation from other populations and from assumptions about density dependence. It is not clear that the uncertainty in these estimates can adequately be described by the notion of variance. Thus, the variances that we used and that we calculated for N_t should not be interpreted as actual estimates of variance for this population.

RESULTS

Bias

The results of the sensitivity analysis of the basic model will be presented by examining the effects of varying each of the variables n, k, and r of Equation (7), separately, and then in combinations.

The sensitivity of the back projected estimates

[5]Smith, T. D., and T. Polacheck. 1977. Uncertainty in estimating historical abundance of porpoise populations. Contract Rep. MM 7A C006, 39 p. Marine Mammal Commission, 1625 Eye Street, Washington, DC 20006.

(S_t) for a fixed number of years t into the past is linear with respect to n or k (Figure 1). This linearity can be seen in Equation (6) since n and k enter only as linear terms in the numerator. Positive values of either n or k yield positive deviations in the back estimates. However, the farther back the population is projected in time, the smaller the contribution of N_0 to the back estimate becomes relative to the contribution of the kills. Thus the effect of bias in the estimate of the initial numbers (n) becomes progressively smaller the farther back in time the population is projected, while the consequence of a consistent bias in the kill estimates (k) becomes larger (Figure 2). Since the annual kills have no simple relationship to time, the effect of a particular value of n or k over time (Figure 2) cannot be described by any simple function. This trade off in the sensitivity of the back projected estimates between n and k is exact in the sense that for any decrease over time in the slope of S with respect to n there is an equivalent increase in the slope of S with respect to k. This can be seen by evaluating the partial derivates of S with respect to n and with respect to k and noting that they sum to 1.

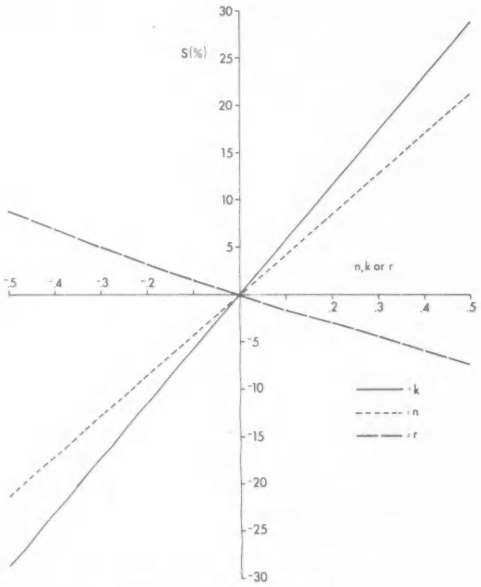

FIGURE 1.—Sensitivity of the model $S_t(n,k,r)$ in 1959 for a range of deviations in the initial number (n), for a range of deviations in the kills (k), or for a range of deviations in the net reproductive rate (r), for *Stenella attenuata* in the eastern tropical Pacific.

The effects of bias in the estimates of the net reproductive rate vector are more complicated than for the other two factors. Positive deviations in the net reproductive rates (r) yield negative deviations in the back projected estimate (Figure 2). The effect of r tends to increase over time (Figure 2). S approaches being linear with respect to r for any particular year, but unlike the relationship for k and n, this result is not exact (Figure 1). The approximate linearity of the sensitivity of N_t

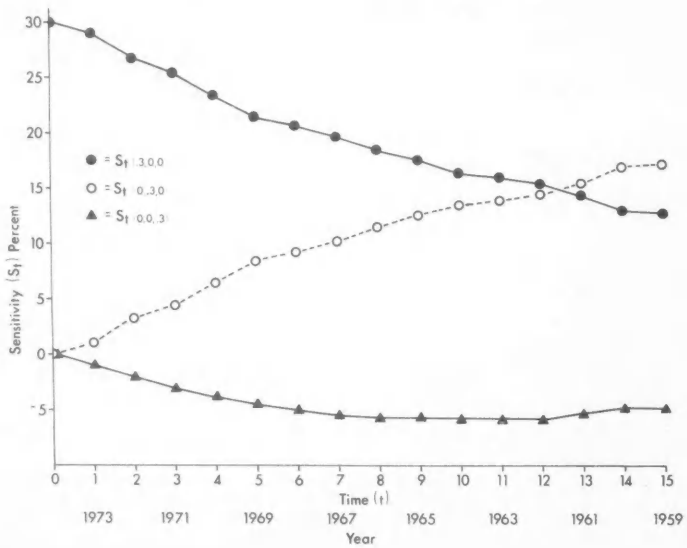

FIGURE 2.—Sensitivity of the model S_t (n,k,r) over time to a 30% deviation in the initial number (n = 0.3), in the kill vector (k = 0.3), and in the net reproductive rate vector (r = 0.3) when all factors are held constant for *Stenella attenuata* in the eastern tropical Pacific.

to r appears to be a general feature of this procedure when r is small. This can be seen by examining S_t expressed as a function of r, which can be obtained explicitly by substituting the definitions of N_t [Equation (4)] and N'_t[Equation (6)] into Equation (7) and simplifying.

The consequences of having two factors varying simultaneously are shown in the series of contours of equal values of S from Equation (7) (Figures 3-5). These contour plots present a visual picture of the sensitivity of the back projection to the different factors. From this set of contour maps, it can be seen that the surface generated by S [Equation (7)] tends to be nearly linear. Since S has no nonlinear terms with respect to n and k, the surface described by S in these two dimensions is simply a plane (Figure 4). There are nonlinear effects between the net reproductive rate and both initial abundance and the sequence of kills. For the example examined here, the nonlinearity between k and r is insignificant. For instance, if r and k both equal 0.50, S deviates from a linear model by <1%. In general the nonlinearity between k and r will be insignificant as long as the kills in any one year do not represent a large proportion of the population and as long as r is relatively small. Also, for the data considered here, the nonlinearity between the net reproductive rates and initial abundance is small but not insignificant. For example, if both n and r equal 0.50, S deviates from a linear model by as much as 5%. This interaction effect is negative, resulting in a surface's bending downward from a strictly linear model when n and r have the same sign.

If all three factors vary together, the surface

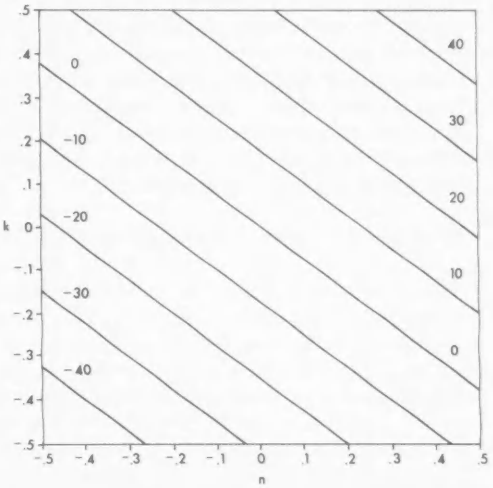

FIGURE 4.—Contours of equal sensitivity of the back estimated abundance in 1959 for a range of deviations in the initial number (n) and in the kill vector (k) when the net reproductive rate vector is held constant for *Stenella attenuata* in the eastern tropical Pacific.

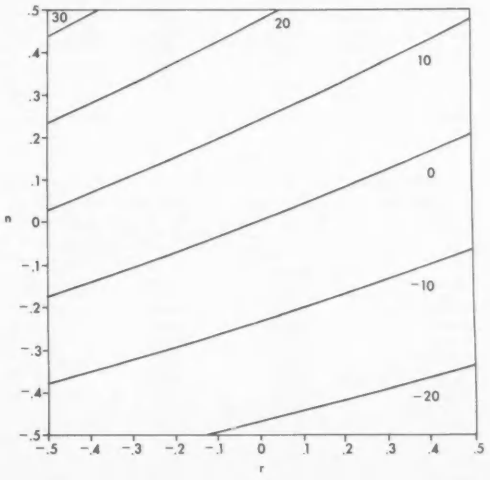

FIGURE 3.—Contours of equal sensitivity of the back estimated abundance in 1959 for a range of deviations in the initial number (n) and in the net reproductive rate (r) when the kill vector is held constant for *Stenella attenuata* in the eastern tropical Pacific.

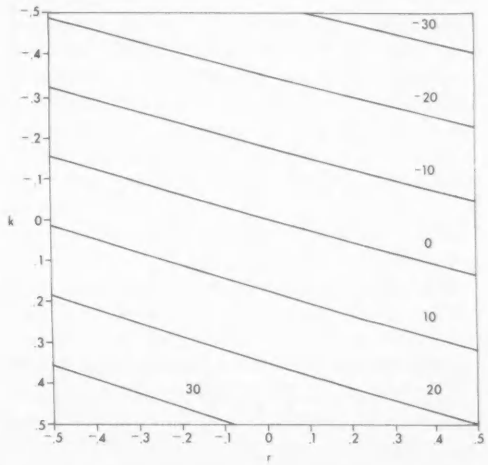

FIGURE 5.—Contours of equal sensitivity of the back estimated abundance in 1959 for a range of deviations in the kill vector (k) and the net reproductive rate vector (r) when the initial number is held constant for *Stenella attenuata* in the eastern tropical Pacific.

generated by S is still relatively linear as there are no terms in S containing n, k, and r and the pairwise nonlinear effects are small as discussed above. Table 2 provides examples of points on this three dimensional surface when n, k, and r are equal in absolute values. It can be seen there, for the example examined, that if the absolute values of n, k, and r are 0.10, the sensitivity of N_{15} ranges from -12 to $+12$.

An empirical equation can be fitted to the sensitivity surface (S) by fitting a linear function for each factor considered independently and by determining a nonlinear term for n and r. The general form of this fitted equation is

$$\hat{S}_t\,(n,k,r) = (b_1K+b_2n+b_3r+b_4nr) \times 100 \quad (10)$$

where the b's are constant. The exact value of the b's depends on the number of years the population is projected back in time. For the example considered here, projecting back from 1974 to 1959, the values of the b's are shown in Equation (11):

$$\hat{S}_{15}\,(n,k,r) = (0.573k+0.427n-0.164r-0.125nr) \times 100. \quad (11)$$

This empirical approximation [Equation (11)] deviates by <2 from the true values of S_{15} for values of n, k, and r <0.5. This emperical equation is useful as the magnitude of the b's provides a measure of the relative sensitivity of the different factors. Thus in Equation (11) it can be seen that for the example considered here the 1959 abundance estimate (N_{15}) is most sensitive to bias in the estimates of the kills. This empirical equation also provides an easy way to generate approximate values of S for any combination of values for n, k, and r.

Variance

The results of the variance calculations for the bridled dolphin are summarized in Tables 3 through 6. Calculated values of the variance of N_t from Equation (9), when all of the random variables are assigned a coefficient of variation of 30%, are given in Table 3, over all years from 1974 to 1959. It can be seen that both the variances and the coefficients of variation (CV) generally decrease. The reduction of the CV over time is due to the fact that the major contributions to the back estimates of the population size are the addition of the kills of the previous years, since the reproductive rate is small. The variance of a sum of independent random variables is the sum of their variances. This always results in a CV for the sum which is smaller than the greatest CV of any of the random variables when the expected values of the random variables are positive (Appendix II). As a generalization, it can be stated that when the net reproductive rate is small the CV of the back estimate will not be larger than the largest CV of any of the random variables, and will usually be smaller.

Table 4 shows the breakdown of the variances calculated in Table 3 into their major components. The variance of N_0 is the major factor in the variance of these back estimates. The contribution of

TABLE 2.—Values of $S_{15}\,(n,k,r)$ when the absolute values of n, k, and r are equal.

Absolute value $\lvert k\rvert=\lvert n\rvert=\lvert r\rvert$	Sign of k	Sign of n: + / Sign of r: +	+ / −	− / Sign of r: +	− / −
0.10	+	9	12	0	3
	−	−3	0	−12	−9
0.20	+	16	23	0	5
	−	16	1	−22	−17
0.30	+	24	36	1	8
	−	−10	2	−33	−26

TABLE 3.—Calculated variance and coefficient of variation for the back estimate of dolphin abundance when all random variables have a CV of 30%.

Year	Variance ($\times 10^{11}$)	CV (%)	Year	Variance ($\times 10^{11}$)	CV (%)
1974	11.03	30.0	1966	7.04	19.1
1973	10.22	29.0	1965	6.9	18.0
1972	9.53	27.0	1964	6.8	17.1
1971	8.88	25.7	1963	6.71	16.7
1970	8.35	23.8	1962	6.67	16.3
1969	7.99	22.1	1961	6.71	15.7
1968	7.56	21.2	1960	6.75	15.2
1967	7.25	20.2	1959	6.75	15.1

TABLE 4.—Breakdown of the variance of N_t into the major components that contribute to the calculated variance.

Year	Contribution to the variance of N_t ($\times 10^{10}$) due to the variance in: The initial number	The kills	The net reproductive rate
1974	110.3	0.00	0.000
1973	101.9	.12	.156
1972	94.2	.76	.305
1971	87.1	.10	.452
1970	81.2	1.755	.568
1969	76.2	2.604	.664
1968	72.1	2.70	.735
1967	68.8	2.91	.784
1966	66.1	3.49	.816
1965	64.1	4.16	.835
1964	62.5	4.64	.843
1963	61.5	4.73	.843
1962	61.1	4.99	.840
1961	61.1	5.24	.840
1960	61.1	5.55	.840
1959	61.1	5.56	.840

TABLE 5.—Coefficients of variation (CV) for the back estimates of bridled dolphin in 1959 (N_{15}) for a range of CV for the parameters of the model. The ranges of CV's of the kills, net reproductive rate, and initial abundances were selected to illustrate particular aspects of the behavior of the variances of the back estimates.

CV of the kills	CV of the net reproductive rate	CV of N_0			
		0	10	20	40
0	0	0	4.7	9.5	19.2
	40	2.2	5.3	9.8	19.3
10	0	1.4	5.0	9.6	19.2
	40	2.7	5.5	10.0	19.4
20	0	2.9	5.6	10.0	19.3
	40	3.7	6.0	10.3	19.5
40	0	5.6	7.5	11.2	20.0
	40	6.2	7.8	11.4	20.2
60	60	9.3	10.5	13.4	21.3
100	100	15.5	16.2	18.2	24.7

the variance of N_0 tends to completely dominate the variance of N_t because of the assumed independence of the kill estimates. Table 5 gives the CV for the back estimated population size of dolphin in 1959 for a range of CV for the different parameters involved in the estimate of N_{15}. As can be seen in this table, unless the variance of N_0 is near zero or unless the CV of the kill and reproductive vectors are extremely large (>60%), the CV of the back estimate does not exceed the CV of N_0.

Comparison of Equations (2) and (3).

A comparison of the estimated back abundance as calculated by the simpler model [Equation (2)] and the basic model [Equation (3)] for the dolphin population examined here is given in Table 6. The simpler model always gives a slightly higher estimate for the size of the back projected population but the increase in the estimate is always <1%. The sensitivities of the two models are nearly equivalent. When the values for the parameters in these models deviate as much as 50% the difference between sensitivities of the two models is <1%. The approximate variances of the back estimates of the two models are also similar.

TABLE 6.—Comparison of the back estimate of the abundance of bridled dolphin as calculated by the basic model [Equation (3)] and the simpler model [Equation (2)].

Year	Simple model ($\times 10^6$)	Basic model ($\times 10^6$)	Simple/basic
1974	3.500	3.500	1.000
1973	3.485	3.483	1.001
1972	3.624	3.617	1.002
1971	3.670	3.659	1.003
1970	3.850	3.835	1.004
1969	4.062	4.0416	1.005
1968	4.115	4.093	1.005
1967	4.214	4.190	1.006
1966	4.412	4.386	1.006
1965	4.640	4.612	1.006
1964	4.840	4.811	1.006
1963	4.934	4.905	1.006
1962	5.021	4.991	1.006
1961	5.467	5.437	1.005
1960	6.001	5.971	1.005
1959	6.130	6.100	1.005

That the difference between the original and the simpler model is small can be shown by analytically comparing the two models. If the projections are made only 1 yr into the past, the ratio of the estimate from Equation (2) to the estimate from Equation (3) is

$$1 + \frac{0.5R_1K_1}{N_0+K_1+0.5R_1K_1}.$$

Only if the value of R_1K_1 is large relative to N_0+K_1 can this ratio deviate significantly from 1. This is only possible if R_1 is relatively large. The general formula for the ratio of the two models is

$$1 + \frac{\sum_{j=1}^{t} 0.5K_jR_j\left(\prod_{h=1}^{j}(1+R_{h-1})\right)}{N_0 + \sum_{j=1}^{t} 0.5K_j\left(\prod_{h=1}^{t}(1+R_{h-1})\right) + \sum_{j=1}^{t} 0.5K_j\left(\prod_{h=1}^{j}(1+R_h)\right)}.$$

As in the case for projecting back only 1 yr, it can be seen that unless the R_jK_j terms are large relative to N_0 and unless the net reproductive rate is also large, the ratio of the two models will be close to 1.

DISCUSSION AND CONCLUSIONS

The results of this analysis indicate that errors in the input parameters do not compound in this procedure for estimating historical abundance. In fact, a systematic bias in the procedure for the estimation of a single set of parameters (either N_0 or R_i's or K_i's) always induces a bias in the back projected estimate which is less than the bias of the estimated parameters. This conclusion follows directly from the linear or near linear relation between S_t and n, k, or r with small rates of change. Moreover, the effects of bias in two or more sets of parameters are nearly additive. The interaction effects of bias in estimates of kills, net reproductive rates, and the initial number tend to

be small or nonexistent. This will be globally true for the relationship between k and n, but will be true for the relationship between k, r, and n only when the net reproductive rate is small. The relative importance of bias in K_i's, R_i's, or N_0 on N_t depends upon the actual values of the parameter. In the bridled dolphin example, after 15 yr, the back estimates were most sensitive to bias in the kill estimate, slightly less sensitive to bias in N_0, and considerably less sensitive to bias in the net reproductive rate. However, the importance of bias in N_0 will diminish with the number of years in the back estimate with a proportionate increase in the importance of bias in the kills.

The sensitivity analysis developed in this paper will include the extremes of a complete sensitivity analysis of the model. The values for $S_t(0,k,0)$ are limiting values to a complete sensitivity analysis of the individual elements of the kill vector on N_t. Similarly $S_t(0,0,r)$ is a limit to complete sensitivity analysis of the individual elements of the net reproductive rate. Given the additivity of S_t with respect to n, r, and k, the surface $S_t(n,k,r)$ contains the extremes of a sensitivity analysis in all $2t+1$ dimensions. If in fact the elements within the kill vector and within the reproductive vector are highly interdependent (as is the case for the data used here), then the sensitvity analysis used to look at the effects of bias in this paper approaches a total sensitivity analysis of the back projected estimate given these constraints.

The variance approximations also indicate that variability in the parameter estimates does not result in compounding uncertainty in the back projected estimates. When estimates of the parameters are independent and the net reproductive rate is low, the CV of the back estimate will be smaller than the CV of the input parameters. In our example if all the CV's were equal, the variance of N_0 would make the largest contribution to the estimated variance of N_t. In general this will be true as long as the kills in any one year do not approach the initial abundance. This is a direct consequence of the basic additivity of the model when the net reproductive rate is small.

In Smith and Polacheck (see footnote 4), an alternative probability structure was considered in which the elements within the kill vector and within the net reproductive rate vector were highly interdependent. In this situation, the variance of N_t is not completely dominated by the variance of N_0. The variances of N_t calculated using this interdependent probability structure are larger than the variances presented here in which all the parameters are assumed independent. However, the CV of N_t for the dolphin data within this interdependent probability structure is still less than the CV of the parameters if all parameters have equal CV. It appears that even in the situation in which a high degree of interdependence exists within the kill estimate or the net reproductive estimates, the variability in the parameter estimates does not induce compounding uncertainty in the back projected estimate.

The comparison of the results from the basic model [Equation (3)] with the simpler model [Equation (2)] indicate that there are no significant differences between the two models as long as the net reproductive rate is small. Thus it appears that there is no reason to favor the more complex model over the simpler.

In conclusion, it appears that this back projection procedure (either model) has reasonable statistical properties, at least when the net reproductive rates are small. However, Equation (1) is a simplified description of how the abundance of a population changes through time, especially in not accounting for changes in age structure. The authors feel that caution should be used in applying estimates from this procedure to the management of long-lived species since changes in the age structure for long-lived species are likely to be important.

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APPENDIX I.—Expressions for the variance components of N_t.

Expression for the right hand terms of Equation (9) are:

$$V(N_0)\left(\frac{\partial N_t}{\partial N_0}\right)^2 = V(N_0)\left(\frac{1}{\prod_{j=1}^{t}(1+R_j)}\right)^2 \tag{i}$$

$$\sum_{j=1}^{t} V(K_j)\left(\frac{\partial N_t}{\partial K_j}\right)^2 = \sum_{j=1}^{t} V(K_j)\left(\frac{1+0.5R_j}{\prod_{h=j}^{t}(1+R_h)}\right)^2 \tag{ii}$$

$$\sum_{j=1}^{t} V(R_j)\left(\frac{\partial N_t}{\partial R_j}\right)^2 = \sum_{j=1}^{t} V(R_j)\left(\frac{N_{j-1}+0.5K_j}{(1+R_j)^2\prod_{k=j+1}^{t}(1+R_k)}\right)^2. \tag{iii}$$

APPENDIX II.—Coefficient of variation of a sum of random variables.

The following is a proof that the coefficient of variation of a sum of two independent random variables is smaller than the greatest CV for either of the random variables if the expected value of the random variables is greater than zero.

If A and B are independent random variables such that

$$E(A) = a>0 \quad E(B) = b>0 \text{ and}$$

$$CV(A) = \frac{\sqrt{V(A)}}{a} \geqslant \frac{\sqrt{V(B)}}{b} = CV(B)$$

then

$$\frac{V(A)}{a^2} \geqslant \frac{V(B)}{b^2},$$

$$V(A)b^2 \geqslant V(B)a^2,$$

$$V(A)(b^2 + 2ab) > V(B)a^2,$$

$$V(A)(b^2 + 2ab) + V(A)a^2 \geqslant V(B)a^2 + V(A)a^2,$$

$$V(A)(a + b)^2 \geqslant [V(B) + V(A)]a^2,$$

$$\frac{V(A)}{a^2} > \frac{V(B) + V(A)}{(a + b)^2} = \frac{V(A + B)}{[E(A + B)]^2},$$

$$CV(A) > CV(A + B).$$

LARVAL DEVELOPMENT OF *GALATHEA ROSTRATA* UNDER LABORATORY CONDITIONS, WITH A DISCUSSION OF LARVAL DEVELOPMENT IN THE GALATHEIDAE (CRUSTACEA ANOMURA)[1]

ROBERT H. GORE[2]

ABSTRACT

The complete larval development of the western Atlantic anomuran crab, *Galathea rostrata*, consists of four or five zoeal stages, and a single megalopal stage, based on larvae cultured under laboratory conditions. Variation in the duration and number of zoeal stages appears to be temperature-dependent, with larvae reared at 15°C developing through five zoeal stages and attaining megalopa in 52 days, whereas larvae cultured at 20°C passed through four or five zoeal stages, reaching megalopa in 18 or 23 days, respectively. At 20°C some third stage zoeae molted to a "regular" fourth zoeal stage, without pleopods, which was followed by a subsequent fifth stage before reaching megalopa. Other zoeae molted to an "advanced" fourth stage, possessing pleopods, which subsequently molted directly to megalopa, bypassing stage V completely. The variation noted in larval development in other galatheid genera is briefly discussed, and a provisional synopsis of morphological characters of systematic value is provided for their identification.

The anomuran crab genus *Galathea* is presently represented in the western North Atlantic by two species, *G. agassizii* and *G. rostrata* (A. Milne Edwards 1880). *Galathea agassizii*, primarily tropical and insular in distribution, is a deepwater species known from 166 to 490 fm (304-897 m) off St. Augustine, Fla., and from Cuba, St. Vincent, St. Lucia, and Barbados in the Caribbean Sea. In the eastern Atlantic the species is found from 82 to 898 fm (150-1,643 m) in the vicinity of both the Cape Verde and Canary Islands, and off northwestern Africa (Chace 1942; Miyake and Baba 1970). Contrarily, *G. rostrata* appears to be a warm-temperate or tropical/subtropical species, primarily continental in distribution. The species is recorded from the North American continental shelf at Cape Hatteras, N.C., to southeastern Florida, and in the Gulf of Mexico from western Florida, the Mississippi Delta, and southward to Islas Jolbos, north of the Yucatan Peninsula. There is a questionable record from off Rhode Island (Williams 1965). *Galathea rostrata* is also found in shallower water than *G. agassizii* and has been collected from 10 to 50 fm (18-92 m), with the exception of the possible depth record of 1,178 fm (2,156 m) from off Rhode Island. The only distributional record of the species for the entire eastern Florida coast was that of Haig (1956) who reported a single specimen collected from 21 fm (38 m) off Hillsboro Lighthouse (Broward County) in southeastern Florida. However, recent collections show that the species is not uncommon in the Indian River region of the central eastern Florida coast, especially on deeper water (60+ m) coquinoid limestone ledges and reefs of the ivory tree coral, *Oculina varicosa* Leseuer.

The few studies made on the larval development of new world galatheid crabs (e.g., Rayner 1935; Boyd 1960; Fagetti 1960; Boyd and Johnson 1963; Fagetti and Campodonico 1971) have all been made on eastern Pacific species, and the larvae of Atlantic American galatheids, including the genus *Galathea*, remain undescribed.

This paper provides the first description and illustration of the complete larval development of *G. rostrata*, as well as the first report on any species of *Galathea* reared totally under laboratory conditions, from hatching to megalopal stage. The larvae and postlarvae are compared with larval stages known from other members of the Galatheidea throughout the world, and shared features are briefly summarized.

MATERIALS AND METHODS

Eight ovigerous females of *G. rostrata* were obtained on 15 April 1977 by lockout diver from the

[1]Scientific Contribution No. 100, from the Smithsonian Institution-Harbor Branch Foundation, Inc., Scientific Consortium, Link Port, Ft. Pierce, Fla. This report is Article IX. Studies on Decapod Crustacea from the Indian River Region of Florida.

[2]Smithsonian Institution, Ft. Pierce Bureau, Ft. Pierce, FL 33450.

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Research Submersible *Johnson-Sea-Link II*, of the Harbor Branch Foundation, Inc. The adult galatheids inhabited a large clump of ivory tree coral which grew in 80 m of water on Jeff's Reef, lat. 27°32.8′N, long. 79°58.8′W, located about 17 n. mi. (27 km) northeast of Ft. Pierce Inlet, Fla. The entire coral colony was collected and returned to the surface inside of a 500-μm mesh cloth bag. Ambient seawater temperature on Jeff's Reef was 12°C at time of collection. The galatheids were immediately placed in compartmented plastic trays containing recently collected neritic seawater previously chilled to 10°C. Upon return to the laboratory each adult specimen was transferred to individual 100 × 80 mm covered glass laboratory dishes filled with approximately 340 ml of seawater previously chilled to 15°C. Each isolated female was maintained at this temperature, provided a change of chilled seawater, and fed freshly hatched *Artemia salina* nauplii, daily. All specimens were exposed to a 12-h light-12-h dark illumination program in a controlled temperature unit (CTU) until hatching occurred. Five females survived in this regimen and yielded larvae over a period from 16 April to 6 May 1977.

Seven larval series were initiated. Using methodology previously described by Gore (1968), five such series were cultured in 24-compartmented plastic trays. These consisted of two series of 8 and 24 larvae, held in the CTU at 15°C (±0.5°C), and three series of 24 larvae each, maintained at cool laboratory room temperature (ca. 20°C, ±1°C). Two mass culture series of about 30 larvae each were also established in individual 100 × 80 mm glass dishes at cool laboratory room temperature, which was controlled by reverse-cycle air conditioning, and was monitored daily with a 7-day recording thermometer. Fresh surfzone seawater (35.5-36‰) was collected weekly, filtered through glass wool, stored in 14-gal (ca. 56-l) polypropylene carboys, and used throughout the rearing period.

All larval series were checked daily, and any molts or dead individuals were recorded and preserved in 70% ethanol. Specimens were examined microscopically, slides prepared, and drawings made as described in previous studies by Gore (1968). Measurements given below are the arithmetic average of all specimens examined in any particular stage. A complete series of larvae, or their molts, is deposited in the National Museum of Natural History, Washington, D.C. (USNM 170862); the Allan Hancock Foundation, University of Southern California, Los Angeles (AHF 1028-01); the British Museum (Natural History), London (BMNH 1978:103); and the Rijksmuseum van Natuurlijke Historie, Leiden (D 31735).

RESULTS AND DISCUSSION OF THE REARING EXPERIMENT

Galathea rostrata passes through four or five morphologically distinct zoeal stages and a single megalopal stage, before completing development in the laboratory. Culture temperature undeniably affects duration of development, and perhaps larval survival as well. While the duration of the zoeal and megalopal stages differed at each rearing temperature, it was nevertheless generally consistent within each of the temperature series, as will be discussed below.

At 15°C five morphologically distinct zoeal stages were observed for those larvae surviving to metamorphosis. The minimum time required to pass through these stages and attain megalopal stage was 52 days. Most larvae remained in each zoeal stage approximately 9-11 days through the first four stages. Only two stage V zoeae survived, and they remained as such 14 and 16 days before molting to megalopa. However, neither of these specimens survived longer than 6 or 7 days as megalopae, so the mean duration of the postlarval stage at 15°C remains unknown (Table 1). With the minimum noted period of 6-7 day duration for megalopae at this temperature, completion of development and metamorphosis to first crab stage

TABLE 1.—Duration of larval and postlarval development in *Galathea rostrata* under laboratory conditions at the indicated temperatures.

Temp and stage	Days required to attain next stage			
	Min	Mean	Mode	Max
15°C:				
I	10	10.8	10	14
II	8	9.7	10	[1]16
III	9	10.5	9	17
IV	8	9.4	9	11
V	14	—	—	16
Mg	6-7	(Both megalopae died in stage)		
20°C:				
I	5	5.8	6	7
II	4	4.2	4	5
III	4	4.1	4	5
IV (regular)	5	5.7	6	6
V (regular)	5	5.8	6	6
IV (advanced)	3	3.3	3	4
Mg (combined)[2]	12	12.6	13	13
III-IV (intermediate)	7	—	—	8 (Died in stage)

[1]One zoea remained 30 days in stage II, dying 13 days later in stage III.
[2]Combined megalopae data include stages obtained from both IV (advanced) and IV (regular).

is conservatively estimated to take well over 60 days (Figure 1).

At 20°C either four or five morphologically distinct zoeal stages occurred. The minimum time required to complete larval development and reach megalopa was 18 days. Most larvae remained in each zoeal stage from 3 to 6 days and as megalopae from 12 to 13 days. The total duration of development from hatching to first crab stage spanned a minimum of 30 days at 20°C, if only four zoeal stages were required, but took at least 37 days with five zoeal stages (Figure 1, inset).

The larvae generally fared well at both culture temperatures. Although the larvae at 15°C took longer to complete their development, they initially appeared to survive better than their counterparts at 20°C (Figure 1). At 15°C, at least 50% larval survival occurred through stage IV, before a rapid decrease occurred in stage V and megalopa. Larvae reared at 20°C exhibited a steep decline after stage 1, to about 35% survival, and showed a continual decline thereafter. The precipitous decline in larval survival at this temperature from stage I to stage II was the result of an almost complete mortality in one culture tray, for unknown reasons.

At 15°C ecdysis in the earlier zoeal stages (I-III) generally was a less critical period than at 20°C, although the larvae at the latter temperature were still able to complete most molts. The larvae at 20°C attained subsequent stages more rapidly than did those at 15°C, and some were able to complete zoeal development, although overall larval mortality was relatively higher. On the other hand, at 15°C larval survival may have been enhanced by lower temperature, but the major difficulty then seemed to be the attainment of stage V and megalopa. Only two megalopae were obtained in the 15°C program and neither was able to molt to the succeeding first crab stage. In contrast, four megalopae survived at 20°C, and molted to crab stage I; three of these specimens were maintained in the laboratory to crab stages XII and XIV.

Ecdysial and Sequential Variation in *Galathea rostrata*

Two modes of developmental variation were noted in *G. rostrata* at 20°C. In one mode, some zoeae III molted to an instar which, for purposes of discussion, is labelled "regular" stage IV. This stage was characterized, among other features, by a reduced number of antennular aesthetascs and was always without well-developed pleopod buds on the abdominal somites. Zoeae remained in this stage for 3-4 days before molting to stage V, an instar possessing distinct, well-developed, pleopod buds and an increased number of antennular aesthetascs. The duration of stage V lasted 5-6 days and was followed by the molt to megalopa. One of these postlarvae subsequently molted to first crab stage.

In the second mode of variation, some zoeae III molted to an "advanced" stage IV, with some, but not all, of the features as noted above for stage V. Zoeae remained longer in the advanced stage (5-9 days) before molting directly to megalopa. Three of these megalopae went on to attain first crab stage. The two types of development are compared in the inset of Figure 1.

Two other stage III zoeae, which remained in stage III 7-8 days (instead of the usual 4-5), molted to what appeared to be an intermediate stage IV. These zoeae exhibited some stage V zoeal features in size, maxillipedal setae numbers, and in possessing pleopod buds, although the latter were only rudimentary. A reduced number of antennular aesthetascs similar to that of regular stage IV zoeae was also seen. The two specimens survived only 4-5 days in this stage before dying. This mode of variation was not considered as important as the previous two modes and will not be discussed further.

Remarks

The regular and advanced fourth stages cannot be equated to an early and late fourth stage, nor to substages IVa and IVb, because no molt occurred from one fourth stage or substage to another. If the molt from stage III was to regular stage IV, this was invariably followed by an ecdysis to stage V, and then a subsequent molt to megalopa. If the molt from stage III produced an advanced stage IV, this in turn molted directly to megalopa, skipping stage V altogether. At 15°C the regular stage IV and stage V appear to be necessary plateaus in larval development, whereas at 20°C development may proceed in some zoeae without resorting to either of these instars.

The regular fourth zoeal stage (as defined above), therefore, appears to be a true sequential stage of development, inasmuch as it was seen in larvae at both 15°C and 20°C programs. However, it is also a stage which can occasionally be skipped

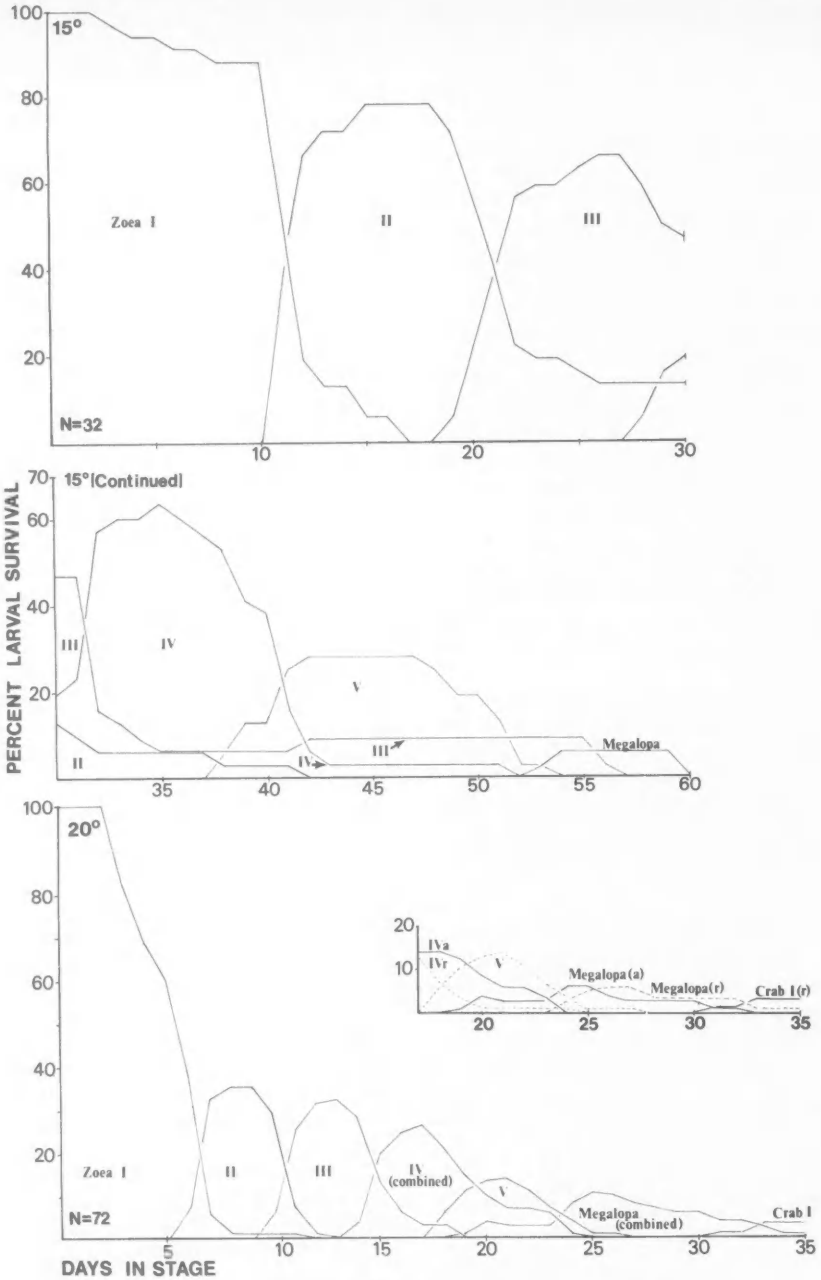


FIGURE 1.—Percentage survival and duration of stages in larvae of *Galathea rostrata* reared under laboratory conditions at 15°C (upper 2 graphs) and 20°C (lower graph). Inset at 20°C gives duration and survival of regular (IVr, dashed line) and advanced (IVa, solid line) stages; number of days the same as in larger graphs.

by some 20°C larvae, and thus could be thought of as an intercalated stage, if the advanced stage IV be considered more indicative of the developmental sequence. Other features shared between the advanced fourth and regular fifth zoeal stages (besides the presence of well-developed pleopod buds noted earlier) include increased numbers of antennular aesthetascs, a remarkable elongation of the antennal endopodite, the appearance of a mandibular palp, and slight changes in setae number on maxillulae, maxillae, maxillipeds, and telsonal uropods (see section on Description of the Larvae). Moreover, the advanced stage IV zoeae were always larger than the regular stage IV zoeae.

It will probably remain a question of semantics whether the regular stage IV is considered an intercalated stage or one that occasionally may be skipped. It could just as well be asked whether the advanced stage IV was an intercalated stage because it embodies many of the features of regular stage IV, plus some seen only in stage V zoeae in the developmental sequence. What is of more importance in the development of *G. rostrata* is that the substitution of an advanced stage IV and the subsequent elimination of the regular stages IV and V allows earlier postlarval metamorphosis. The resultant early benthic crab stages may be reached in a shorter period of time by the species, thereby reducing the time spent in the plankton.

Discussion

It is, of course, conjectural as to whether the larvae of *G. rostrata* skip stages in their development in the natural environment or are ever subject to constant low (e.g., 15°C) or intermediate (20°C) seawater temperatures. The adults of the species, found in deeper continental shelf waters, presumably are often exposed to cool seawater temperatures, as was noted, e.g., during the time the adult females for this study were collected. It is not unreasonable to assume that developmental stages may occasionally be subjected to relatively constant cool temperatures as well, either immediately after hatching or just prior to postlarval metamorphosis when the megalopae settle to the sea floor. In addition, should the larvae become entrained in cyclonic cold core rings of Gulf Stream origin (see Richardson 1976; Wiebe 1976; Wiebe et al. 1976), they would presumably be subjected to relatively constant cold water (at least 17°C) for at least part of their developmental period. Delayed metamorphosis provides an alternative hypothesis against the more traditional "stepping-stone" idea, to account for the rather extensive distribution of the species along the Middle and North American continental shelves.

There is some evidence that larvae of other species of *Galathea* may skip stages in the plankton (Lebour 1930, 1931) and that other galatheids may intercalate substages (e.g., Boyd and Johnson 1963). For example, the larvae of four of the five British galatheids described by Lebour, viz. *Munida rugosa* (Fabricius 1775 [as *M. banffica* = *M. bamffica* (Pennant 1777)]), *Galathea intermedia* Lilljeborg 1851, *G. squamifera* Leach 1814, and *G. strigosa* (Linnaeus 1767) developed through four zoeal stages, whereas *G. dispersa* Bate 1859, exhibited four or five stages. Lebour (1930) considered five stages in the latter species as "probably normal" but pointed out that the megalopa could be obtained from the fourth [numerical] stage, and "the normally fifth [numerical] stage has been seen to emerge from the third stage." She stated that the fourth or fifth stage may therefore be omitted in *G. dispersa*, but made no mention of intercalated stages or substages.

The developmental situation in *G. dispersa* is quite similar to that noted in this report for *G. rostrata*, in which an advanced fourth stage replaces the regular fourth and fifth stages, thereby causing them to be omitted from the developmental sequence. Lebour's (1930) "fifth stage. . . from third" is probably equivalent to what is termed in this report the advanced fourth stage. Her statement that long, unjointed pleopods appear in the "last" stage of *G. dispersa* indicates that either the fourth stage (or advanced) or fifth stage (or regular) possess these appendages, depending on whichever stage is "last." It also indicates that the molt to megalopa does not occur without the appearance of pleopods in the "last" larval stage. However, North Sea species of *Galathea* differ from *G. rostrata* in possessing pleopod primordia "in the third stage" which are "long but unjointed in the last stage" (Lebour 1930). In addition, Sars (1889) had also noted and illustrated pleopod development in the "last" stage of larvae attributed to *G. intermedia*, *Munida rugosa*, and *Munidopsis* [as *Galathodes*] *tridentata* (Esmark 1857). The latter species will be considered further below.

Rayner (1935), using planktonic stages from Argentinian waters, described the larvae he attributed to *Munida gregaria* (Fabricius 1793) and

M. subrugosa (White 1847). Rayner did not note any substages or skipped stages in the five instars he described for the two species, and was not certain whether additional stages followed. By analogy with *M. rugosa* [as *M. bamffica*] he thought it possible that the next stage would be postlarval. In this he was probably correct, but it seems strange in retrospect that Rayner did not attach importance to the well-developed pleopods on the larvae before him, a feature by which he earlier characterized the fifth zoeal stage. These appendages in other galatheid larvae are quite obviously developed at stage V (see Lebour, Sars, Boyd and Johnson, and others), and Sars (1889) even drew attention to them when describing his "last zoeal stage."

Intercalation of substages, however, is known in the genus *Pleuroncodes*, as was specifically discussed by Boyd and Johnson (1963) in the larvae of *P. planipes* Stimpson 1860.[3] Five zoeal stages had been initially noted in this species (Boyd 1960), but a sixth stage, apparently unnatural and not known to occur in the plankton, could be induced in the laboratory. Boyd and Johnson thought this stage was due to the presence of penicillin pills or to the $CaCO_3$ buffer in the pills, used to control bacterial growth in the cultures. These authors also stated that numerical stage IV could be subdivided into a complex of from four to nine substages, each represented by a molt, all without pleopods, but otherwise morphologically similar to each other. Although no sequential substages were skipped (e.g., a molt from substage IVa to IVh), one or more substages could be omitted terminally, with a subsequent molt to the morphologically discrete stage V, which possessed pleopods (Boyd 1960). Boyd and Johnson suggested that in *P. planipes* the number of substages in stage IV was probably influenced by temperature, with higher culture temperatures (e.g., 16°-20°C) producing faster development but causing more substages to occur before the molt to stage V. They noted, however, that other factors such as food supply or crowding of larvae might also exert an effect on the number of substage instars, but neglected to consider the possibility that the large number of induced substages in stage IV might also be due to the use of antibiotics in the cultures, as suggested by Fagetti and Campodonico (1971).

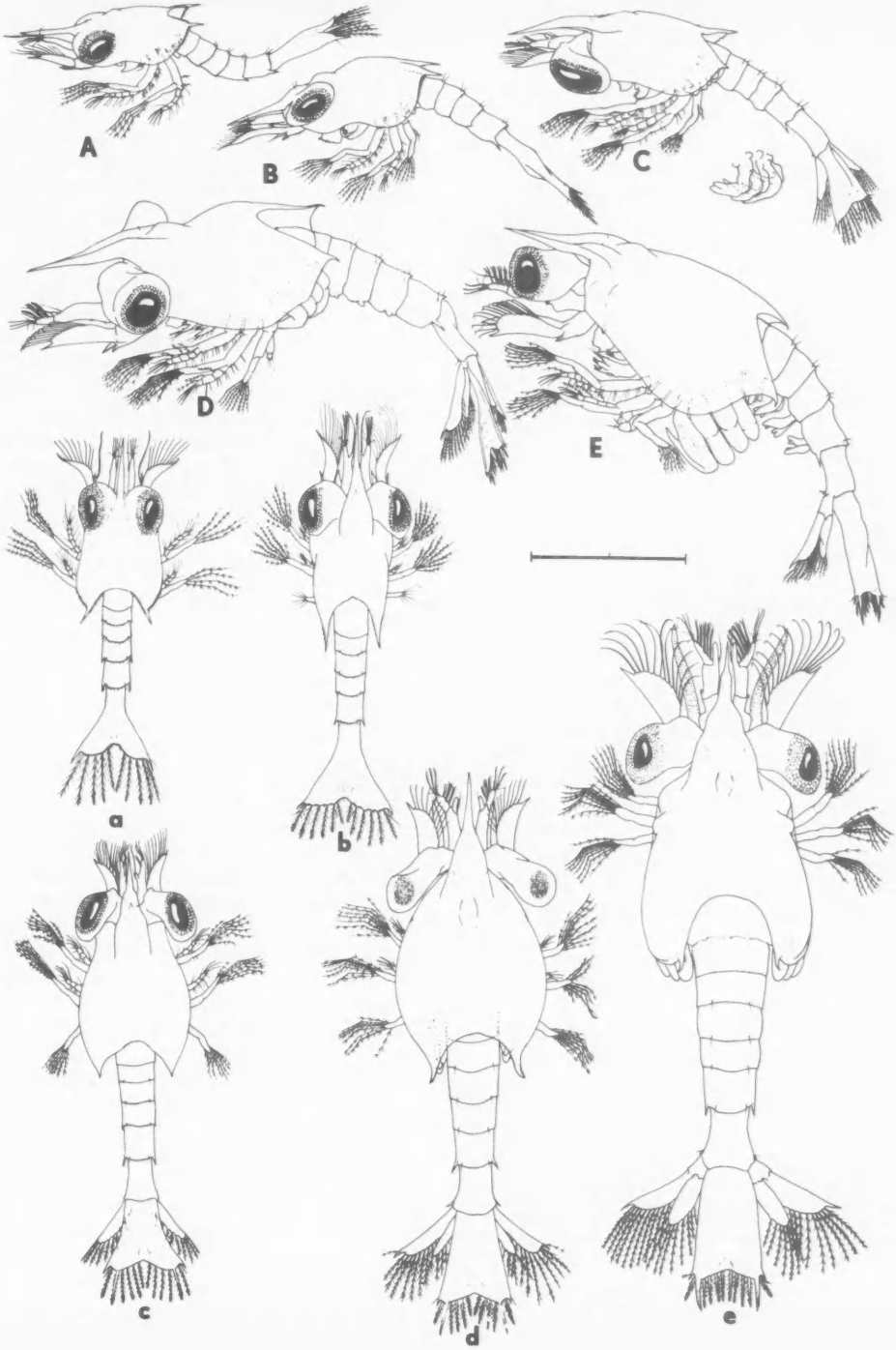
[3]Both Stimpson (1860) in his original description of *Pleuroncodes planipes* and Haig (1955) have suggested that the species may prove to be only a northern Pacific form of the Chilean *P. Monodon*.

FIGURE 2.—*Galathea rostrata*, zoeal stages in lateral and dorsal view: (A, a) First zoea; (B, b) second zoea; (C, c) third zoea; (D, d) fourth zoea (regular); (E, e) fifth zoea. Scale line equals 1.0 mm.

The Chilean congener, *Pleuroncodes monodon* Milne Edwards 1837, also was found to have intercalated substages (Fagetti and Campodonico 1971). At 15°C, substage IVa-d were followed by a molt to stage V, possessing pleopods; at 20°C a fifth substage (IVe) was attained instead of zoeal stage V. Whether stage IVe would be followed by ecdysial stage V is not known because all larvae in stage IVe died. However, the lack of pleopods in stage IVe implies that stage V should occur, with pleopods, before the molt to megalopa takes place. Whether such substages occur in the plankton is conjectural, but they certainly would present some difficulty in separation because of their great similarity to each other in samples collected from the plankton.

Abbreviated larval development is also known to occur in at least two galatheids. Sars (1889), in describing the prezoel, "first" and "last" zoeal stages of *Munidopsis tridentata* from Norwegian waters suspected that development time was shorter than that seen in *Galathea*, but came to no conclusion as to the total number of stages. He commented on the remarkably advanced features exhibited in the early zoea, an observation later supported by Samuelsen (1972). Samuelsen determined that only three zoeal stages exist for *M. tridentata* and further suggested that the megalopal stage followed stage III because the latter stage was in the same relative state of development as some fourth zoeae which preceded the megalopae in other galatheids. Samuelsen noted that the presence of a mandibular palp, pleopod primordia, antennular aesthetascs, antennal setae, and scaphognathite setae in the early zoeal stages were all advanced features usually restricted to later zoeae in other galatheid larvae. The relatively nonsetose feeding appendages and endopodites of the natatory appendages indicate that the larvae may not feed, although they can swim well.

Al-Kholy (1959) described and figured larvae attributed to a "*Galathea* sp." which apparently developed through only three zoeal stages. However, no methodology was given, nor indication as to whether the larvae were cultured in the laboratory or collected from the plankton. It is doubtful whether the species will ever be identi-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fiable based on his incomplete descriptions and rather stylized illustrations.

Advanced development[4] is implied in but one galatheid, the cave-dwelling *Munidopsis polymorpha* Koelbel 1892. This species is presently known only from a littoral cave formed by lava tunnels which connect to the sea in the Canary Islands (Fage and Monod 1936). These authors never found more than five, extremely large (1.5-1.8 mm in diameter) eggs on an individual female. No larval stages were described, but it was hypothesized that the young *Munidopsis* was well advanced in development inside the egg and probably hatched into a form nearly like the adult. Given the rather unique habitat for a *Munidopsis*, advanced development in *M. polymorpha* would not be surprising. The vast majority of other species of *Munidopsis* are deep-sea forms, most of which occur below 500 m (Mayo 1974) in the Atlantic Ocean, although some species occur in shallower waters on the continental shelf.

In summary, it is apparent that larval development in the Galatheidae is quite diverse, including advanced development (i.e., with imminent metamorphosis) in the cave dwelling *M. polymorpha*, abbreviated development with as few as three larval stages (*M. tridentata*, Al-Kholy's *Galathea* sp.?), to "normal" development of four-five zoeal stages (e.g., *Munida*, *Galathea*). Substage intercalation is known in the genus *Pleuroncodes*, but seems to be restricted to the fourth, or penultimate, ecdysial stage. Intercalation of a sixth zoeal stage, perhaps only a laboratory artifact, is also known in one species of this genus. Skipped stages appear only in two species of *Galathea*, and perhaps one of *Munida*, at present, and these result in the elimination of regular zoeal stages IV and V and their replacement by an advanced stage IV which subsequently molts directly to megalopa.

Developmental variation such as that just discussed allows some interesting speculation as to its evolutionary consequences in view of the fact that the phylogenetically closely related anomuran family Porcellanidae generally undergo a reduced developmental sequence of usually no more than two zoeal stages. These stages appear to be morphologically equivalent in most respects to *Galathea* stages I and IV, sensu lato. Substages have been postulated for some porcellanid larvae, notably Indo-Pacific species, but are not positively known to occur in Atlantic and eastern Pacific species. Previously postulated substages in Atlantic species have been shown to be the result of accelerated morphological development without an ensuing molt and have been seen primarily in larvae collected from the plankton (Gore 1968 and others). However, the larvae of the western Pacific genus *Petrocheles* apparently do reflect their galatheid ancestry by undergoing five zoeal stages during development. Morphological features of the telson, uropods, and antennal scale in these larvae all resemble, to a greater or lesser degree, their counterparts in larvae of *Galathea* and *Munida* (Wear 1965). Further studies along these lines should be most interesting and productive.

DESCRIPTION OF THE LARVAE

First Zoea

Carapace length: 1.0 mm.
Number of specimens examined: 10.

Carapace: (Figure 2A, a). Typically galatheid, somewhat inflated; rostral spine horizontal, little expanded proximally, straight, extending to level of scapherocerite spine, or slightly beyond, about 0.5× carapace length(CL), unarmed; posterolateral carapace margins armed with a series of about 15 small denticles placed before large, posterior spine; latter slightly more than 0.1× CL; dorsomedial carapace margin excavated, with about 13 small denticles along sinus margin. Two small setae medially above eyes; latter sessile.

Antennule: (Figure 3A). A simple rod, both endopodite and exopodite fused to protopodite; former with 1 elongate plumose seta, latter with 3 aesthetascs and 3 setae.

Antenna: (Figure 3B). Endopodite rodlike, about 0.4× scaphocerite length, fused to protopodite, a single distinct spine at its tip, plus a long plumose seta; scaphocerite usually with 9 setae along margin, tip produced into long daggerlike spine about 0.3× total scale length; protopodite

[4]The term "direct" development is restricted in this paper to those larvae which hatch from the egg in a form morphologically similar to the adult and undergo no further metamorphosis. Larvae exhibiting "advanced" development usually hatch in the penultimate or ultimate zoeal stage and thus may undergo additional ecdysis prior to metamorphosis. Larvae with "abbreviated" development hatch as early zoeae (often with a prezoeal or first zoeal stage present), but may dispense with one or more intermediate stages in completing their larval development.

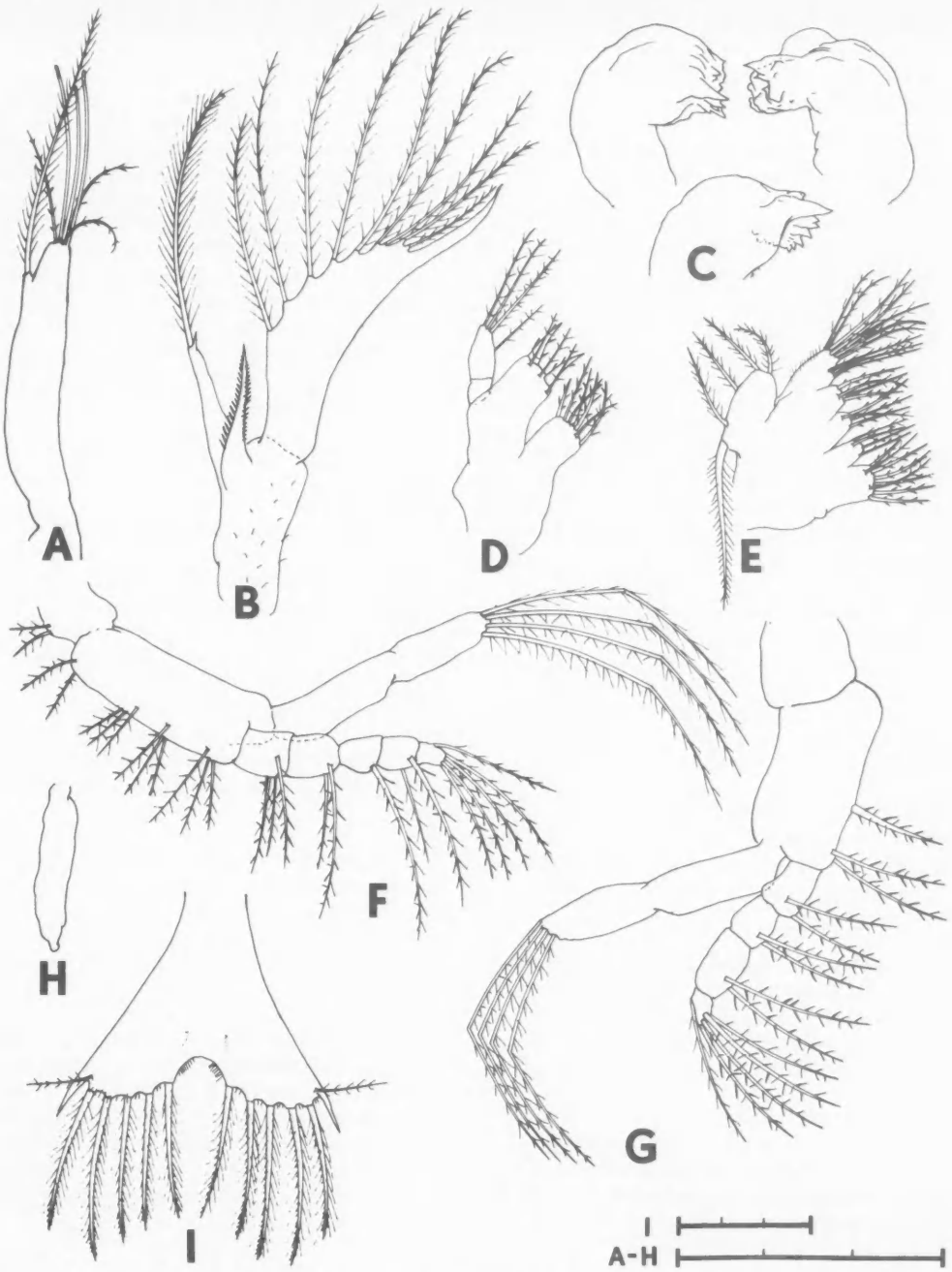


FIGURE 3.—*Galathea rostrata*, first zoeal appendages: (A) Antennule; (B) antenna; (C) mandibles, lower view rotated interiorad to zoea to show dentition; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxillped 2; (H) maxilliped 3; (I) telson. Scale lines total 0.3 mm.

with sharply pointed spine ventrally, armed along either side with distinct acute spinules; this spine falling short of distal tip of endopodite; scattered setae basally on protopodite.

Mandibles: (Figure 3C). Asymmetrical dentate and spined processes, as shown.

Maxillule: (Figure 3D). Endopodite segmented, 3 terminal, 1 subterminal seta. Basal endite with 2 large, widely separated strong spines, plus 3 setae; coxal endite with 4 spines, 3 strong setae.

Maxilla: (Figure 3E). Endopodite setae, progressing subterminally, 3-4, 3, plus 3 laterally, and additional fine hairs as illustrated. Basal endite proximal and distal lobes each with 3 regular and 1 spinelike seta; coxal endite proximal and distal lobes with 8, and 4 spinelike setae, respectively. Scaphognathite with 4 lateral, 1 stout elongate apical seta.

Maxilliped 1: (Figure 3F). Coxopodite with 2 setae. Basipodite setae formula progressing distally 2, 3, 3, 3. Endopodite five-segmented, setae progressing distally 3, 2, 1, 2, 4 + I (Roman numeral denotes dorsal setae); all endopodal and basipodal setae heavy, spikelike. Exopodite two-segmented, 4 natatory setae.

Maxilliped 2: (Figure 3G). Coxopodite naked. Basipodite setae 1, 2, progressing distally. Endopodite four-segmented, setal formula 2, 2, 2, 4 + I; all spikelike. Exopodite two-segmented, 4 natatory setae.

Maxilliped 3: (Figure 3H). A small, unsegmented amorphous bud.

Pereiopods: Appear as small and undifferentiated buds, gradually enlarging as stage progresses.

Abdomen: (Figure 2A, a). Five somites; last 2 with large lateral spines; somites 2-5 each with paired setae dorsally, plus a series of small distinct spinules along posterior margin of somite; somite 6 fused to telson. Pleopods absent.

Telson: (Figure 3I). Setal formula on margin 7 + 7; all plumose setae (= processes 3-7) with small, hooklike spinules progressing down their length; other setae and hairs as illustrated. Anal spine absent.

Color: Zoea transparent; frontal region of carapace diffused with orange, brighter orange dorsally on midgut region. Chromatophores as follows: orange on protopodite of antennule, faintly orange on scaphocerite of antenna; red-orange around inner oral region; mandibles and labrum outlined in red, interiorly orange; basipodites of maxillipeds 1 and 2 red-orange along dorsal and ventral margins; red spiderlike chromatophores dorsally in longitudinal line on abdominal somites 3-5; orange chromatophores ventrally placed in a similar manner. Eyes black, with bluish highlights in reflected light.

Second Zoea

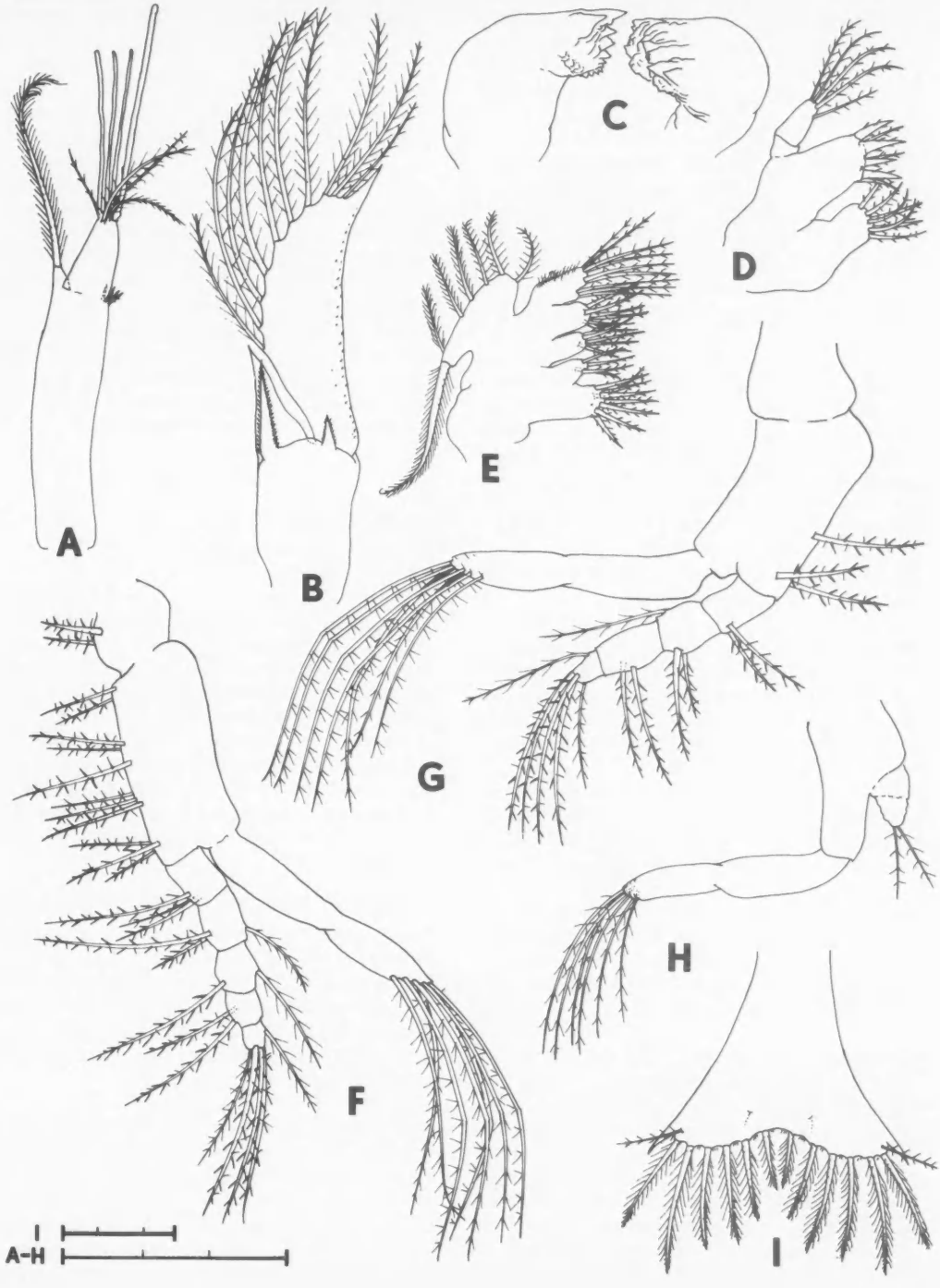
Carapace length: 1.2 mm.
Number of specimens examined: 8.

Carapace: (Figure 2B, b). More inflated; rostral spine more or less knifelike in lateral view, noticeably expanded proximally in dorsal view; about 0.5× CL, overreaching distal tip of antennal scaphocerite spine in several specimens, unarmed; posterolateral margins of carapace with about 14 small denticles or spinules, dorsomedial margin possessing only scattered nubs or with denticles totally absent; posterior spines remain slightly more than 0.1× CL; eyes now stalked.

Antennule: (Figure 4A). Incipient segmentation seen at junction of exopodite with protopodite; former usually carrying 4 aesthetascs and setae, with 4 small thick setules on junction with protopodite. Endopodite retains single long plumose seta.

Antenna: (Figure 4B). Endopodite thickened, drawn into point distally, appearing conical, about 0.3× scaphocerite length, incompletely fused to protopodite, now lacking elongate plumose seta seen in first stage. Scaphocerite usually with 10 marginal setae, plus numerous small spinules ventrally along outer margin; distal spine about

FIGURE 4.—*Galathea rostrata*, second zoeal appendages: (A) Antennule; (B) antenna; (C) mandibles; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) telson. Scale lines total 0.3 mm.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0.2× scale length. Protopodite now carries second sharp spine ventrally, armed as first along outer margins; larger ventral spine now shorter than endopodite; ventral spinulelike setae inconspicuous or lacking.

Mandibles: (Figure 4C). Dentition now larger, more complex. No palp.

Maxillule: (Figure 4D). Endopodite unchanged from stage I. Basal endite with 4 large spines, 3 setae; coxal endite processes stronger, but number unchanged, from stage I, appearing to be 5 spines, 2 strong setae.

Maxilla: (Figure 4E). Endopodite setal formula progressing subterminally 4, 2, plus 3 laterally, and fine hairs as shown. Basal endite proximal and distal lobes with 4-5, 6 processes, respectively, former as 3-4 spinelike and 1 thin seta, latter as 1 strong and 1 regular spine, 4 thin setae. Coxal endite distal lobe with 3 spines, 1 strong seta, proximal lobe with 8 spines or strong spinelike setae. Scaphocerite with 6 lateral, plus usual elongate apical seta.

Maxilliped 1: (Figure 4F). Coxopodite and basipodite setae unchanged from stage I. Endopodite setal formula now 3, 2 + I, 1 + I, 2, 4 + I. Exopodite remains two-segmented throughout later development, now with 7 natatory setae.

Maxilliped 2: (Figure 4G). Coxopodite and basipodite as in stage I. Endopodite setal formula 2, 2 + I, 2, 5 + I. Exopodite as above and for later stages, carrying at this stage 7 natatory setae.

Maxilliped 3: (Figure 4H). Remarkably developed; incompletely two-segmented exopodite with 6 natatory setae; endopodite poorly calcified, originating about half way up basipodite, two-segmented, with 2 terminal setae.

Pereiopods: (Figure 2B). Undifferentiated, but enlarging buds throughout stage.

Abdomen: (Figure 2B, b). Five somites, sixth still fused to telson; lateral spine on somite 5 distinct, that of somite 4 reduced, even vestigial; paired dorsal setae on posterior dorsal margins of somites 2-5 remain, and are present throughout later zoeal stages; posterior marginal spinules much reduced in size and number.

Telson: (Figure 4I). Marginal setal formula 8 + 8, additional pair added in medial sinus; latter reduced from distinct U-shaped notch seen in stage I. Armature on plumose processes as before, but distal tips with hooklike processes more distinct; other setae and hairs as shown.

Color: Similar to stage I, but with less diffusion of orange frontally; internal midgut region, mandibles and maxillipedal basipodites retain red-orange color, mandibles showing noticeable red outline, maxillipedal color appearing more diffused than stage I; abdominal somites 4-5 with red dorsal and lateral chromatophore lines, plus orange line ventrally, all connecting to single orange ring of spiderlike chromatophores around each anterior margin of somites 4 and 5. Eyes electric blue to black in reflected light.

Third Zoea

Carapace length: 1.3 mm.
Number of specimens examined: 8.

Carapace: (Figure 2C, c). Proximal margins of rostral spine more developed laterally when seen dorsally, in this and subsequent stages; length remains about 0.4-0.6× CL, distal tip reaches to about tip of scaphocerite spine or slightly beyond; posterolateral margins of carapace with denticles much reduced, becoming irregular nubs; dorsomedial margin with only poorly developed, ragged nubs, almost totally obsolete; posterior carapace spines considerably shortened, less than 0.1× CL. Eyes much enlarged, basal peduncles elongate.

Antennule: (Figure 5A). Exopodite segmented from protopodite, bearing 2 lateral aesthetascs in addition to 3 terminal, plus 3 or 4 setae, at tip. Endopodite slightly enlarged, retaining long plumose seta. Protopodite carries single long lateral seta distally, plus 2 short fine setae, placed medially, and basally, and 4 short stout setae distally.

Antenna: (Figure 5B). Endopodite continues to develop, but remains incompletely segmented from protopodite, now about 0.5-0.6× scaphocerite length, a thin seta just below spinous tip. Scaphocerite with 9-11 marginal setae, number somewhat variable on left and right appendages in same specimen, plus additional shorter spinules

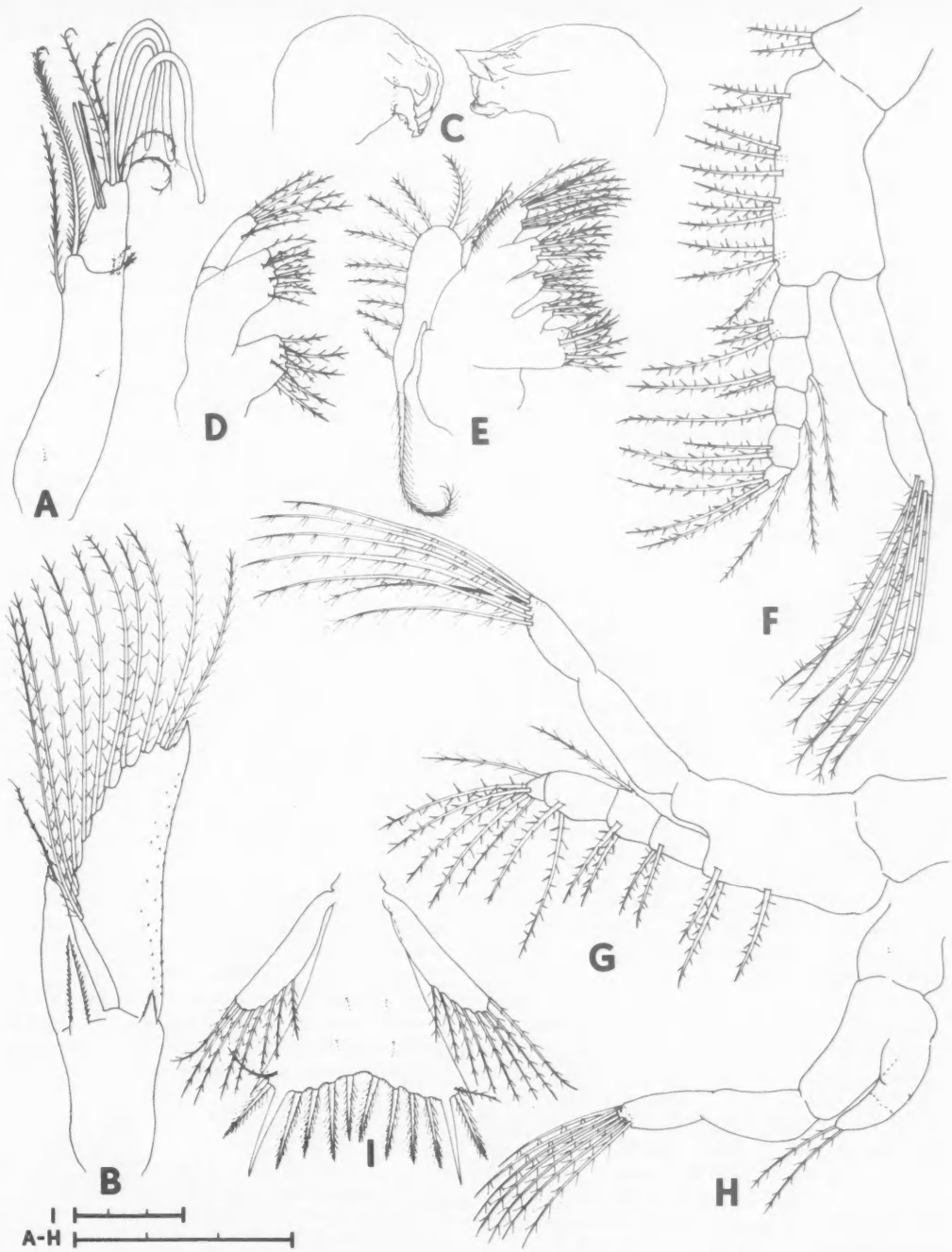


FIGURE 5.—*Galathea rostrata*, third zoeal appendages: (A) Antennule; (B) antenna; (C) mandibles; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) telson. Scale lines total 0.3 mm.

along ventral outer margin; distal spine shortened to about 0.1× scale length. Protopodite retains 2 sharp ventral spines, larger about 0.6× endopodite length, smaller about 0.3× length of larger.

Mandibles: (Figure 5C). Incisor and molar processes more developed; no palp.

Maxillule: (Figure 5D). Endopodite unchanged. Basal and coxal endites both with 5 spines, 3 setae.

Maxilla: (Figure 5E). Endopodite unchanged. Numbers and form of processes on either endite little changed from earlier stage, with exception of basal endite distal lobe; latter now with 1 spine, 4 strong setae, 1 thin seta. Scaphognathite with 10 marginal setae and usual thick apical seta.

Maxillipeds 1 and 2: (Figures 5F, G). Coxal, basipodal, dorsal and ventral endopodal, and exopodal natatory setae as in previous stage.

Maxilliped 3: (Figure 5H). Endopodite bud now subequal to basipodite length, incipient segmentation more prominent in some specimens than others; exopodite with 7 natatory setae.

Pereiopods: (Figure 2C, and detailed inset). More developed, many with incipient segmentation; partial chelation of protochela often visible.

Abdomen: (Figure 2C, c). Six somites present, sixth divided from telson; distinct lateral spine remains only on somite 5; spinules on dorsal posterior margins vestigial, ragged and irregular. In some specimens small, amorphous swellings occur ventrally on somites 2-5, signifying future position of pleopod buds.

Telson: (Figure 5I). Marginal setal formula remains 8 + 8; fourth pair of processes elongate spines fused to telson; processes 3, 5-8 retain noticeable hooklike spinules distally; other dorsal setae as illustrated. Uropods present at junction of abdominal somite 6 and proximal margin of telson; exopods of same well developed, with variable number of marginal plumose setae (usually about 8); endopods, if present, merely foreshortened naked buds.

Color: More distinctly colored than stage II. Orange chromatophores: dorsally on interior margin of eyestalks, a single orange spot on carapace laterally, just above each maxilliped 1, another small grouping laterally on abdominal somite 2; diffused orange on antennular peduncle, ventrolaterally on carapace below eyes, interiorly on mouthparts and within gut region, and on endopodites of maxillipeds 1-3. Red chromatophores: on cutting edge of mandibles, dorsomedially and laterally on abdominal somite 4, laterally on somite 5, the latter appearing as if small drops of blood.

Fourth Zoea (Regular)

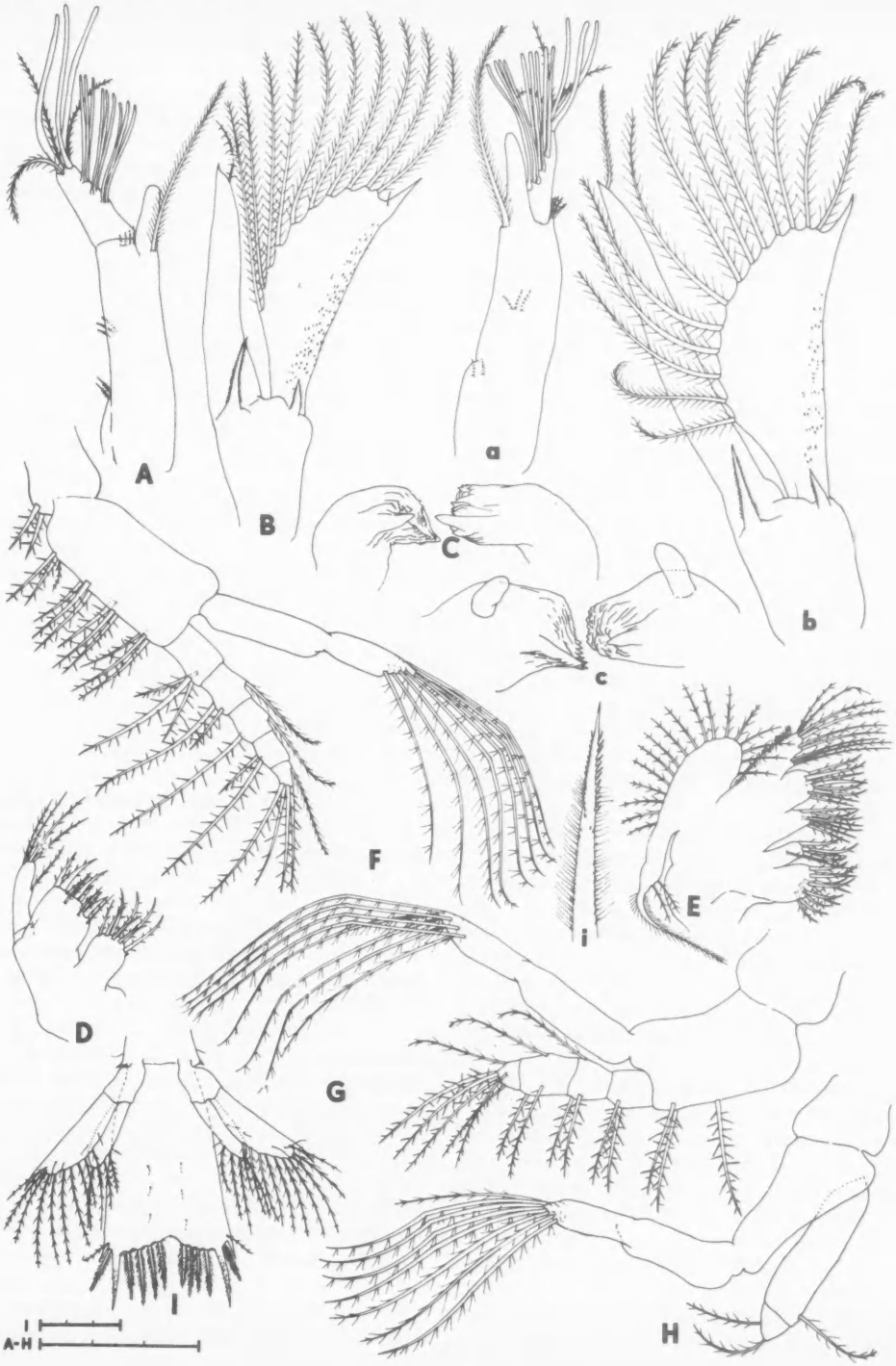
Carapace length: 1.4 mm.
Number of specimens examined: 10.

Carapace: (Figure 2D, d). Rostral spine with noticeably raised lateral margins, greatly expanded basally at point of attachment to carapace, slightly overreaching scaphocerite spine and antennular exopodite; carapace posterolateral and dorsomedial margins unarmed; posterior spines quite short, hooked downward. Eyes large, on elongated stalks.

Antennule: (Figure 6A). Exopodite with three rows of lateral aesthetascs, numbering distally 2-3, 3, 2-3, in addition to usual 3, plus 3 setae, at tip. Endopodite about 0.5× length of exopodite, plumose seta absent. Protopodite retains distal lateral setal, plus usual 4 stout setae at junction of exopodite; 3 medial, 2 basal setae now also present.

Antenna: (Figure 6B). Endopodite elongate subequal to scaphocerite length; latter bearing 10-12 (numbers variable on left and right appendages in same specimen) marginal setae plus numerous ventral spinules on outer margin. Larger protopodal ventral spine about 0.3× endopodite length, smaller about half size of larger; armature of both remains as in earlier stages.

FIGURE 6.—*Galathea rostrata*, fourth zoeal appendages: (A) Antennule, regular stage; (a) same, advanced stage; (B) antenna, regular stage; (b) same, advanced stage; (C) mandibles, regular stage; (c) same, advanced stage; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) telson; all regular stage; (i) detail, fifth telsonal process, 40× objective. See text for discussion. Scale lines total 0.3 mm.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Mandibles: (Figure 6C). Molar and incisor processes acutely spinous, otherwise unchanged from earlier stages; no palp.

Maxillule: (Figure 6D). Endopodite unchanged, but may have small seta at base of segment. Basal endite with 7 stout spines, 3 setae; coxal endite with 5 or 6 long spines, 3 strong setae, and occasional small tooth.

Maxilla: (Figure 6E). Endopodite unchanged. Basal endite distal lobe with 6 spines, 2 setae, proximal lobe with 7 or 8 spines and strong setae intermixed; coxal endite distal lobe with 4 terminal spines, 1 lateral seta, proximal lobe with 11 spines, placed 5 terminally, 4 subterminally, 2 laterally. Scaphognathite with 17-20 marginal setae, including 2 or 3 anteriorly near base, plus usual long apical plumose seta, as shown.

Maxilliped 1: (Figure 6F). Basipodite adds a single small seta proximally, ventral formula now 3, 3, 3, 3. Endopodal and coxal setae unchanged; 8 exopodal natatory setae.

Maxilliped 2: (Figure 6G). Coxal and basipodal setae unchanged. Endopodite setal formula 2, 2 + I, 2 + I, 5 + I. Exopodal natatory setae 8.

Maxilliped 3: (Figure 6H). Endopodite overreaches basipodite, bearing 3 setae. Exopodite with 8 natatory setae.

Pereiopods: (Figure 2D). Chelation and segmentation more or less apparent, progressing rapidly throughout stage; entire pereiopodal mass hangs from beneath posterolateral carapace region in later stage.

Abdomen: (Figure 2D, d). Lateral spine present only on somite 5; dorsal spinulation on posterior margins of somites nearly absent; paired dorsal setae remain. A short, sharp spine on posterolateral margin of somite 6, just above insertion of uropodal basipodite. Pleopod primordia may be present in some specimens, but development is weak and occurs slowly, if at all, throughout stage.

Telson: (Figure 6I, i). Uropods completely developed, exopodite distal outer tip produced into long spine, 8-11 long marginal setae present; endopodites with 4 or 5 setae; with shorter setae on both rami. Telson marginal setal formula 8 + 8, fused fourth process now heavily spinulose, other movable processes (except process 2, which, as in other anomurans, remains a simple seta) carry distinctive, sharp, separated, spinules along their length (Figure 6i; 40× objective), these spinules much more hooklike distally, more spinous proximally. Other dorsal and ventral setae on telson as illustrated.

Color: Similar to stage III; quite developed and noticeable along anterior and internal margin of eyestalks; interiorly on midgut, and bases of maxillipeds; single red chromatophores now basally on antennular protopodite, on posterior margin of maxillipedal basipodites, and laterally on abdominal somites 3-5; eyes blue, reflecting green highlights.

Remarks: This stage, with limited aesthetasc numbers, reduced antennular endopodite and unsegmented protopodite, lacking mandibular palps, and with developing pereiopods and usually only pleopodal primordia, always molted to zoeal stage V.

Fourth Zoea (Advanced)

Carapace length: 1.6 mm.
Number of specimens examined: 12.

Carapace: Differs little from regular stage IV except being larger, more inflated; armature similar to regular stage zoea.

Antennule: (Figure 6a). Endopodite about 0.75× to nearly equal to length of exopodite; latter with four rows of aesthetascs laterally, as 1, 3, 3, 2, plus usual 3, plus 3 setae terminally. Other setae as illustrated.

Antenna: (Figure 6b). Endopodite distinctly overreaches (1.2×) scaphocerite; latter with 12-14 marginal setae; larger ventral propodal spine about 0.25× endopodite length, remaining half again as long as smaller propodal spine.

Mandibles: (Figure 6C). Large, heavily toothed processes, distinguished now by undivided simple palp.

Maxillule: May add one more process on basal endite; tooth on coxal endite usually distinct.

Pereiopods: Well formed, completely segmented and chelated, protruding almost totally from under posterolateral carapace margins.

Abdomen: Somites 2-5 each with a pair of undivided pleopod buds, gradually lengthening as stage progresses, but never becoming bifid.

Color: Similar to regular stage IV zoeae.

Remarks: The zoeae in this stage are much more developed morphologically, possessing a different arrangement of antennular aesthetascs, a well-developed antennal endopodite, mandibular palps, segmented and chelated pereiopods, and distinct (but undivided) pleopod buds. These zoeae molt directly to megalopae, bypassing stage V completely.

Fifth Zoea

Carapace length: 1.6 mm
Number of specimens examined: 8.

Carapace: (Figure 2E, e). Rostral spine with lateral margins appearing somewhat embossed at posterolateral angle of zoeal orbit; carapace lateral margins deeply rounded, convex posterolaterally, unarmed; posterior spine recurved ventrally in some specimens, nearly straight in others, inner margin of same curving regularly inward to deeply excavated dorsomedial margin of carapace; latter entirely without armature. Eyes large, ovoid, on well-developed elongate stalks.

Antennule: (Figure 7A). Exopodite with five rows of aesthetascs laterally: 2, 3, 3, 3, 2, plus 3 and 3 setae at tip. Endopodite from about 0.75× to just subequal in length to exopodite. Protopodite segmented into elongate basipodite and truncated coxopodite; former with a single long plumose seta distally, plus 4 stout setae terminally at exopodite junction, 3 more medially; latter with 2 stout setae ventrally near line of segmentation.

Antenna: (Figure 7B). Endopodite very noticeably longer than scaphocerite (1.3-1.4×); latter bearing 12-14 plumose marginal setae plus additional ventral marginal spinules as in earlier stages. Larger propodal ventral spine less than 0.2× endopodite length, smaller remains about half the size of larger, both armed similarly as illustrated. Toward end of larval stage transparent endopodite reveals distinctly segmented megalopal antennal flagellum within endopodal sheath.

Mandibles: (Figure 7C). Noticeably dentate, each with simple, distinct palp.

Maxillule: (Figure 7D). Endopodite unchanged from regular stage IV; basal setule may not be present. Basal endite with 8 stout spines, 3 setae; coxal endite with 6 long spines, 3 strong setae, and small tooth, placed as illustrated.

Maxilla: (Figure 7E). Endopodite unchanged. Basal endite distal lobe with 8 spines and strong setae, 2 thin setae terminally, one regular seta laterally; proximal lobe with 6 terminal, 2 subterminal, 2 lateral processes, most appearing to be strong setae and spines. Coxal endite distal lobe with 2 spines, 2 strong apical setae, 2 thinner subapical or lateral setae; proximal lobe with about 13 spines and strong setae, progressing terminally to laterally as 7, 4, 2. Scaphognathite with about 22-25 marginal setae, including enlarged plumose seta apically; 2 small setules present, positioned laterally.

Maxilliped 1 and 2: (Figures 7F, G). Little changed from previous stage.

Maxilliped 3: (Figure 7H). Little changed in form from previous stage, except endopodite now much larger, longer, extending well past distal margin of basipodite; 3 setae as before.

Pereiopods: (Figure 2E). Extremely large, appearing to be nearly functional, protruding beneath, and forcing posterolateral margins of carapace, outward; walking leg segmentation and cheliped chelation distinctly visible.

Abdomen: (Figure 2E, e). Lateral spine on somite 5, and that on posterodistal angle of somite 6, the only armature. Pleopods present as well-developed, bifid, buds.

Telson: (Figure 7I, i). Uropods well-developed, both endopodite and exopodite with variable number of marginal setae, usually 8-10, and 10-13 or occasionally 14, respectively. Telsonal fused and movable processes as illustrated; fourth process distinctly spinulose; occasionally an extra

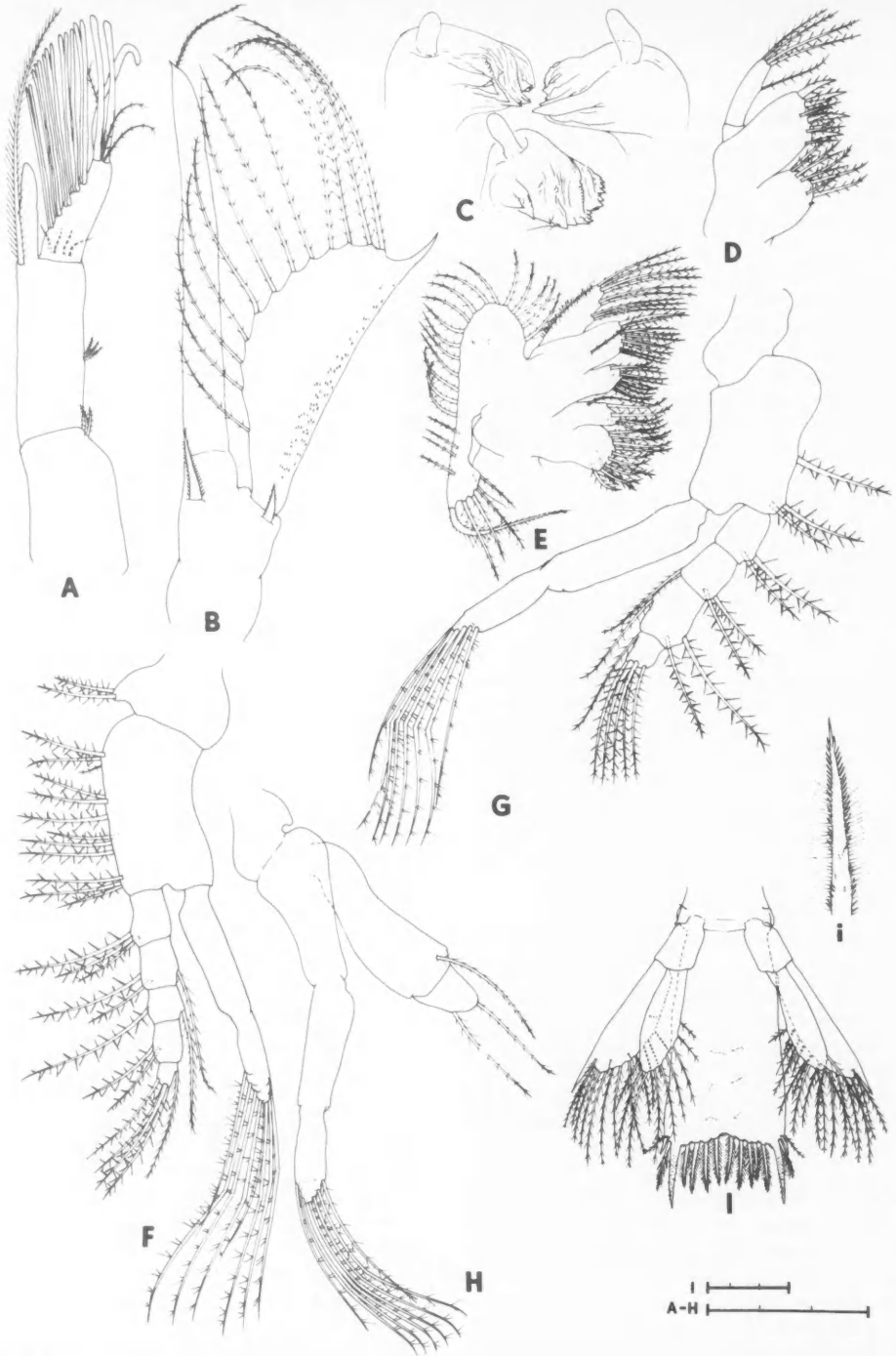
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FIGURE 7.—*Galathea rostrata*, fifth zoeal appendages: (A) Antennule; (B) antenna; (C) mandibles, lower view rotated exteriorad of zoea to show dentition; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) telson; (i) detail (40 × objective), fifth telsonal process. Scale lines total 0.3 mm.

plumose process appears making telson marginal setal formula 8 + 9 as shown.

Color: Chromatophores as follows: Red, on anterior margin of eyestalks, paired on carapace dorsally just behind eyes on frontal region, single ventrolaterally beneath each eyestalk just above mandibular region, ventrally on both antennular and antennal peduncles at junction with carapace, laterally on carapace above insertion of maxilliped 2; interiorly on mouth region on outer margin of mandible, posterior to mandible on maxillule, and on midgut; abdominal somites 3-5 with several groups laterally, plus a reddish-orange line above hindgut of same. Orange chromatophores in elongate streaks longitudinally on basipodite of maxillipeds 1-3, more diffused on maxillipedal endopodites, and in lateral groupings on abdominal somites 3-5. Eyes blue-green in reflected light, corneas dark, probably black.

Remarks: This stage followed the regular stage IV and invariably molted to megalopal stage.

Megalopa

Carapace length × width: 1.7 × 1.2 mm.
Number of specimens examined: 4.

Carapace: (Figure 8A, B). Resembling miniature adult; rostrum triangular proximally, drawn into sharp point distally, armed along lateral margins with 4 distinct spines, some smaller spinules occasionally interspersed; frontal region with additional spinules as illustrated; 2 elongate thickened setae on gastric region, plus other setae and spinules as shown; lateral margins with 4 large spines, including 1 at epibranchial angle, 2 placed about equidistant behind, and the fourth at junction with cervical groove; a variable number, usually 3, smaller spines laterally between larger spines; a fifth large spine on posterolateral margin, followed by another, smaller, dorsally and posteriorly. Numerous small setae scattered over entire carapace; eyes each with 2 large, feathery setae on anterodorsal margin.

Antennule: (Figure 9A, a). Biramous; peduncle large, three-segmented; basal segment inflated, with 2 large forward-directed spines dorsally, another, smaller, distoventrally; other setae as shown; remaining two segments nearly smooth, sparsely setose. Lower ramus three-segmented, tip with 2 spinules (see detail, Figure 9a), other setae as shown. Upper ramus six- or occasionally indistinctly seven-segmented; aesthetascs on segments two through five in the following sequence of rows and numbers: one row (2), two rows (3, 3, + 2 setae), two rows (3, 2, + 1 seta), one row (2); sixth segment with a single elongate terminal seta plus other smaller setae.

Antenna: (Figure 9B). Peduncle three-segmented, heavily spined; flagellum with 2 or 3 fused segments plus a variable number (about 24) shorter segments each bearing 5 or 6 setae distally; terminal segment with 7 longer setae, as illustrated.

Mandible: (Figure 9C). Symmetrical, scoop-shaped process, chitinized along leading margin; a three-segmented palp, basal segment of which bearing 2 short, spinelike setae, third segment with about 13 or 14 stout, toothed spines.

Maxillule: (Figure 9D). Endopodite now possessing but a single short, terminal seta. Basal endite with 4 strong terminal setae, followed by 16 short, stout spines, 4 subterminal and 3 lateral setae; a single seta basally as shown; coxal endite lower portion extended into elongate, weakly chitinized, lobe fringed with fine hairs; 3 basal setae, 3 lateral setae, followed by 11 stout spines and 8 strong setae terminally.

Maxilla: (Figure 9E, e). Endopodite with a single, long subterminal seta. Coxal and basal endites heavily spinose and setose, numbers and position difficult to discern, but approximately as follows: basal distal lobe, about 14 terminally, 4 + 2 subterminally, 2 laterally; proximal lobe, about 6 terminally, 3 + 1 subterminally, 1 + 2 laterally; coxal distal lobe, about 3 each, terminally and subterminally, 2 + 8 in irregular row laterally; proximal lobe, about 11 placed more or less terminally, 8 subterminally, 22 in a row encircling lobe laterally, 1 + 2 beneath these; for exact positioning refer to outer (Figure 9E) or inner (Figure 9e) views of lobes. Scaphognathite with about 40

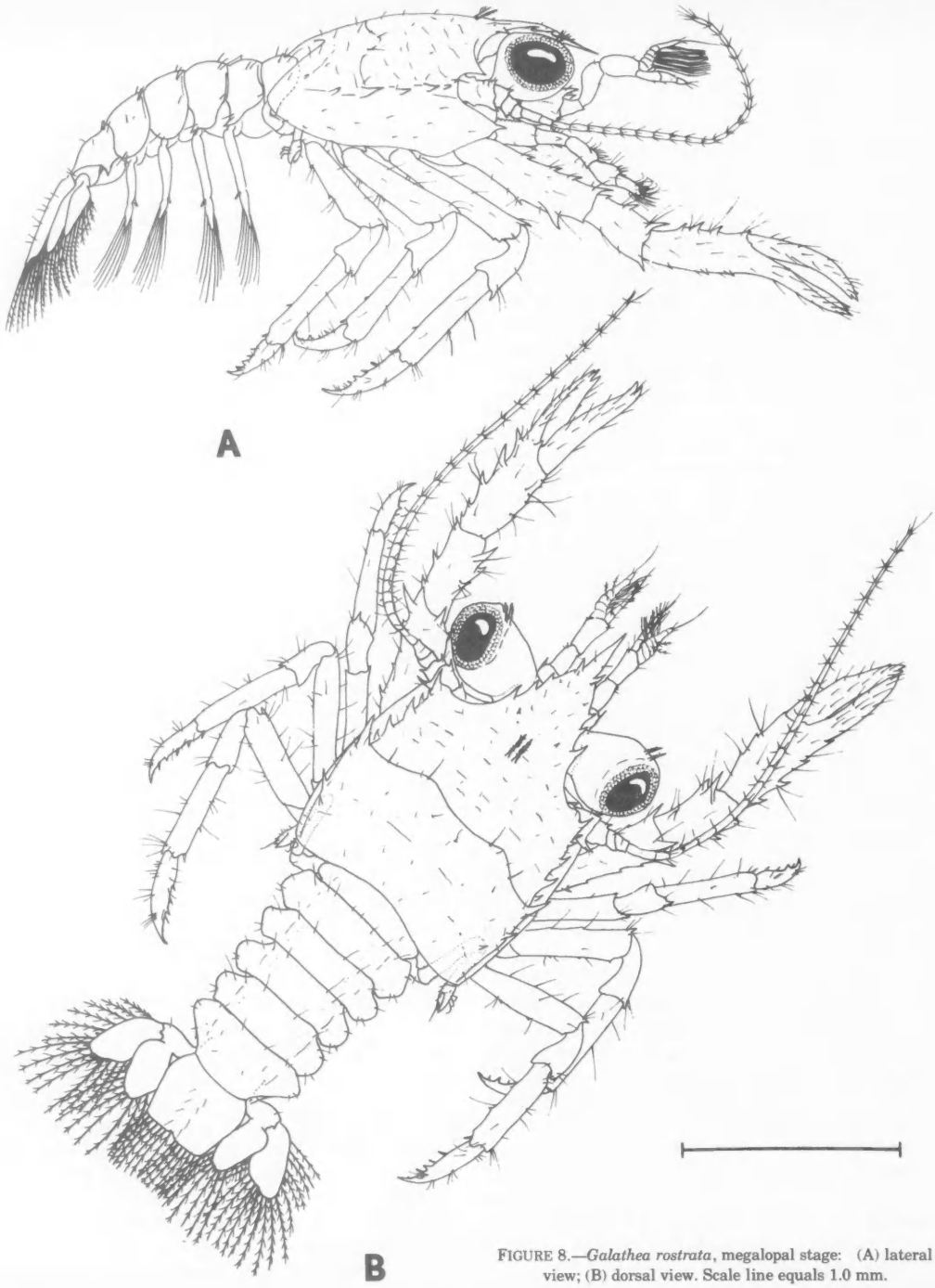

FIGURE 8.—*Galathea rostrata*, megalopal stage: (A) lateral view; (B) dorsal view. Scale line equals 1.0 mm.

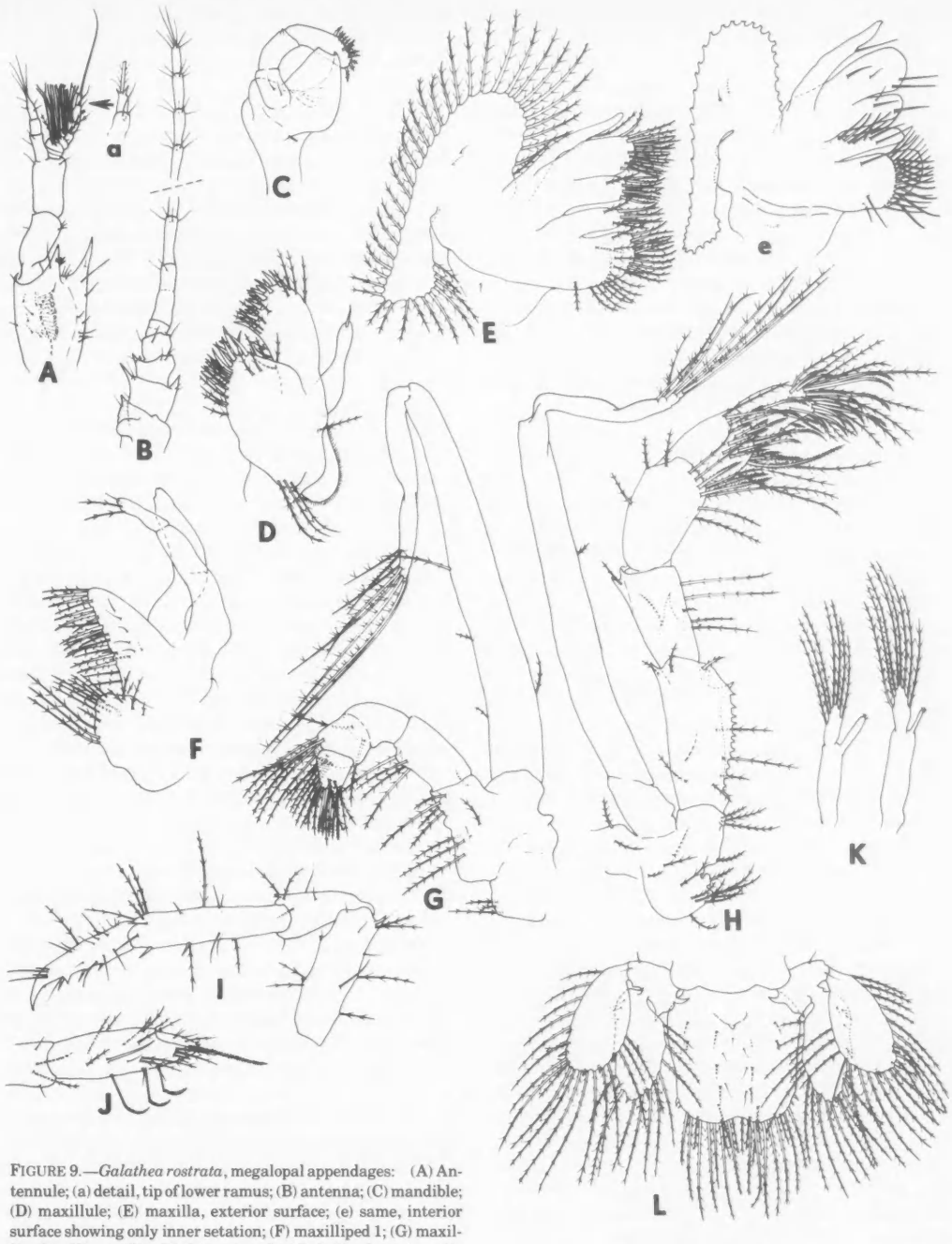

FIGURE 9.—*Galathea rostrata*, megalopal appendages: (A) Antennule; (a) detail, tip of lower ramus; (B) antenna; (C) mandible; (D) maxillule; (E) maxilla, exterior surface; (e) same, interior surface showing only inner setation; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3; (I) pereiopod 4; (J) cheliped, pereiopod 5; (K) pleopod 1 (right) and 4 (left); (L) tail fan. Scale lines total 0.3 mm.

marginal setae plus finer setules on either side of upper lateral surface.

Maxilliped 1: (Figure 9F). Exopodite and endopodite weakly chitinized; former two-segmented, with 3 more or less terminal setae; latter naked. Protopodite with about 27 and 15 setae on basal and coxal endites, respectively, placed as illustrated.

Maxilliped 2: (Figure 9G). Exopodite two-segmented, 8 terminal, plus other setae, as shown. Endopodite four-segmented, proximal two with 4 and 2 setae, respectively, distal two each with about 12 processes, including 5 daggerlike spines terminally. Setae on basipodite and coxopodite as illustrated.

Maxilliped 3: (Figure 9H). Exopodite two-segmented, 8 terminal setae. Endopodite five-segmented; ischium and merus each with strong, sharp triangular spine, plus a shorter spine at anterodistal angle; ischium also with prominent crista dentata; last three segments (carpus, propodus, dactylus) with 3, about 15, about 18 long daggerlike spines plus numerous longer setae interspersed among them. Several setae on coxopodite and basipodite.

Pereiopods: (Figures 8A, B; 9I, J). Chelipeds rounded, equal, elongate, heavily spined, covered with long, stiff bristlelike setae, these more prominent in gape of fingers and on outer surface of manus; fingers of each hand trifid at tips. Merus and carpus with marginal spines. Walking legs thin, elongate; merus, carpus, and propodus covered with setae plus small spinules ventrally along margins, these often difficult to discern except under higher (40× objective) magnification; propodus with 2 larger spinules ventrally; dactylus with 3 large movable spinules plus one fixed triangular tooth on ventral margin; a second, very small, almost vestigial tooth may appear about midway between larger fixed tooth and dactylar tip. Pereiopod 5 chelate, 1 long serrated seta, 3 scythelike pectinate setae quite noticeable, plus additional numerous setules on manus; 2 very small, spinulelike teeth on distal tip of dactylus.

Pleopods: (Figures 8B, 9K). Occur on somites 2-5; biramous, greatly elongate; exopodal setae progressing toward telson 8, 8, 8, 7, with minor variation of 1 or 2 occasionally seen on left or right side in same specimen; endopodites not as long as exopodites, thin, naked, but each with appendix interna of 2 or 3 small hooks developed at tip.

Tail Fan: (Figure 9L). Telson with 6 or 7 long plumose setae, and several shorter marginal setae interspersed among these, numbers of latter inconsistent in same specimen; 1 or 2 small toothlike spines laterally, as shown. Uropods biramous, each with 4 widely separated marginal spines, that on outer lateral margin of endopodite the strongest; exopodite with about 18-20, endopodite blade with 11-14 plumose marginal setae, numbers again variable in same specimen. Smaller setae on dorsal and ventral surfaces of tail fan as illustrated.

Color: Megalopa beautifully colored. Carapace and abdomen overall red-orange, dorsolateral carapace margins and spines darker red; an irregular longitudinal white, or semitranslucent stripe extends dorsally from just behind frontal region along entire length of carapace and abdomen; this stripe bordered with darker orange-red chromatophores along its length; a similar white stripe appears laterally, below which carapace becomes translucent, but covered with numerous red spiderlike chromatophores; a third stripe appears ventrally on sternum, extending to junction of abdomen. Numerous pale blueish-white dots interspersed over dorsal surface of carapace, especially on either side of previously noted longitudinal stripe. Eyestalks orange-red, with regular white band longitudinally, this meeting second band which encircles distal margin of eyestalk just before cornea; latter black, overlain with dark red maculations. Chelipeds with distal margin of merus, entire carpus, propodus, and all but distal tip of dactylus ivory white; merus proximally red-orange; cheliped finger tips orange. Walking legs translucent, speckled with many red-orange chromatophores, these coalescing to form irregular bands on outer segments; dactyli of latter clear, or light horn color.

DISCUSSION

In the western North Atlantic Ocean the family Galatheidae is represented by four genera: *Galathea* (2 species), *Munida* (31 species), *Munidopsis* (48 species), and *Phylladiorhynchus* (1 species). With the exception of the present report, the larval development of the remaining 81

galatheid species known to occur in the western Atlantic is unknown.

The majority of our knowledge on galatheid larvae comes from studies conducted on species from the eastern Atlantic and Pacific Oceans, and associated seas such as the Red, Mediterranean, or North Seas. Lebour (1930) first characterized larvae in the family Galatheidae, and Gurney (1942) was the first to provide a synopsis of larval features based on Lebour's work and studies he made on western Pacific galatheid larvae. As might be expected, only some of the characters considered important by Gurney in 1942 remain valid today, and the lack of detailed descriptions in earlier studies on galatheid larval morphology prevents comparative statements to be made among most of the species for which the larvae are known. Nevertheless, morphological differences in rostral, carapacial, antennal, abdominal, and telsonal features continue to be of some value in distinguishing the larvae of at least five galatheid genera.

In general, the larvae so far described for species of *Munida* share several features with those known from *Galathea* and *Pleuroncodes*, and are thus somewhat indicative (as seems true for the adults) of close relationships among the three genera. *Pleuroncodes*, an eastern Pacific genus, is morphologically very similar to *Munida* in several larval features, more so than are larvae of *Galathea* as presently described. As noted in the following synopses, the larvae of the three genera can be easily separated. The adults, based on present taxonomic criteria, are distinct and generic status is undoubtedly warranted.

The genus *Munidopsis*, on the other hand, is a heterogeneous grouping of forms, some adults bearing little resemblance to others in the taxon (see Mayo 1974, for discussion). The larvae from the sole species so far described, however, are certainly distinctive and do not resemble those from other genera. The genus *Munidopsis*, as presently constituted, would seem to provide an ample example of a taxon wherein the relationships among the various species (and perhaps their elevation to generic status) might be clarified on the basis of morphological relationships among their larvae.

The first zoeal larvae of the eastern Pacific species *Cervimunida johni* (Fagetti 1960) are quite spinose but could perhaps be confused with either *Munida* or *Pleuroncodes* larvae (Fagetti and Campodonico 1971). It remains to be seen whether later larval stages would be more distinctive. The presence of a single ventral antennal spine (instead of two as seen in other genera) is of limited value, because *Galathea* and *Munida* exhibit a single spine in stage I and two spines in later stages (see below).

In the genus *Galathea*, larvae are principally known from northeastern Atlantic species described by Lebour (1930, 1931) and Sars (1889). Live specimens of these species may be separated from larvae of *G. rostrata* by chromatophore color and position, but unfortunately no further detailed comparison is possible until the former species are completely redescribed and illustrated. This holds true for most of the studies by the 19th and early 20th century authors which were listed in Gurney (1942). The "*Galathea* sp." briefly described and illustrated by Al-Kholy (1959) from the Red Sea agrees in several respects with "typical" *Galathea* larvae, but differs in others. Whether it may be equated with Gurney's (1938) *G. longimana* remains uncertain as the brief descriptions and illustrations of both authors prohibit meaningful comparison between the two studies, and those on other *Galathea* larvae.

In order to facilitate comparison between the two western Atlantic *Galathea* species a summary of larval features exhibited by *G. rostrata* is provided in Table 2. These may be applied both to *G. agassizii*, when its larvae become known, and to other *Galathea* larvae when expanded or more complete descriptions are provided. In addition, a provisional synopsis of larval characters for the five genera discussed above is also presented. The summaries have been extracted from the more reliable larval descriptions, as so noted, and may allow distinction among the more typical larvae in each genus. As our knowledge increases further modification may be required.

SYNOPSES OF GALATHEID LARVAE

In the following section, emphasis is placed on the setal-spinal formulae of the larval telson. Conventionally, this formula may be expressed thusly: 8 + 8, indicating that eight telsonal processes, consisting of fixed and movable spines, setae, and thin hairs, occur on each side of the telsonal midline. It is apparent now that the type of these processes may provide a useful reference feature in distinguishing between the various galatheid larvae. Accordingly, spines (whether movable or fixed) are herewith denoted by Roman

TABLE 2.—Summary of zoeal features in the larval stages of *Galathea rostrata*.

	Zoea I	Zoea II	Zoea III	Zoea IV (regular)	Zoea IV (advanced)	Zoea V
Rostral spine	Not expanded proximally	Expanded proximally	Expanded proximally	Raised lateral margins	As in regular stage	Expanded proximally
Posterior carapace spines	Elongate	Elongate	Reduced	Slightly hooked	Slightly hooked	Hooked
Eyes	Sessile	Stalked	Stalked, enlarged	Stalked, elongate	Stalked, elongate	Stalked, greatly developed
Antennule	Simple rod, no lateral aesthetascs Endopod reduced	As in stage I Endopod more developed Protopod lacks lateral seta	Exopodite segmented, 2 lateral aesthetascs Protopod with 1 lateral seta	3 lateral rows aesthetascs Endopod ½ exopod length Protopod unsegmented	4 lateral rows aesthetascs Endopod subequal to exopod	5 lateral rows aesthetascs Endopod subequal to exopod Protopod segmented
Antenna	Exopod with seta Scaphocerite spine elongate	Exopod lacks seta Scaphocerite spine reduced	Exopod ½ scaphocerite length, with apical seta	Exopod subequal to scaphocerite, with apical seta	Exopod longer than scaphocerite with apical seta	Exopod much longer than scaphocerite with apical seta
Mandibles	Without palp	Without palp	Without palp	Without palp	Palp present	Palp present
Maxillipeds:						
Endopod (1)	3,2,1,2,4+I	3,2+I,1+I,2,4+I	As in previous stage	and thereafter		
Endopod (2)	2,2,2,4+I	2,2+I,2,5+I	2,2+I,2,5+I	2,2+I,2+I,5+I	As in previous stage	and thereafter
Endopod (3)	Bud	Less than basipod, 2 seta	Subequal to basipod, 2 seta	Longer than basipod, 3 seta	As in regular stage	Much longer than basipod, 3 seta
Exopods (1, 2)	4	7	7	8	8	8
(3)	0	6	7	8	8	8
Pereiopods	Amorphous buds	Developing buds	Developing buds	Well-formed buds	Segmented, chelated buds	Large, nearly functional
Abdomen	5 somites, lateral spines 4, 5 Pleopods absent	5 somites, spine on 4 reduced Pleopods absent	6 somites, spine on 4 vestigial Pleopods absent	6 somites, spine on 4 absent Pleopod primordia may be present	6 somites Pleopods present, undivided	6 somites Pleopods present, bifid
Uropods	Absent	Absent	Exopods present Endopods rudimentary	Exopods and endopods developed	As in previous stage	and thereafter
Telson	7+7 setae 4th process movable	8+8 setae 4th process movable	8+8 setae 4th process fused	8+8 setae As in previous stage and thereafter	8+8 setae	8+8 setae

numerals, setae by Arabic numerals, and fine hairs by lower case Roman numerals. It should also be remembered that previously movable setae may, in a subsequent stage, become fixed spines and the setal formulae will change accordingly. Thus, a setal configuration proceeding medially of a fixed spine (I), a thin hair (ii), a regular seta (3), a previously movable seta now a fixed spine (IV), followed by four movable setae (5-8) results in the telsonal formula of I + ii + 3 + IV + 5-8. While somewhat more ponderous than the previously used formula of 8 + 8, it does provide a clearer picture of the type of processes and their changes throughout subsequent larval development.

Cervimunida (Fagetti 1960)

Rostrum elongate, needlelike, noticeably denticulate; carapace posterolateral and posterior margins dentate; posterior spines extremely elongate, reaching fifth abdominal somite; antennal scaphocerite elongate, aciculate, distinctly spined along outer margin, and upper surface, basal segment with a single dorsal spine, unarmed ventrally (thus differing noticeably from other galatheids where the situation is exactly the reverse); abdominal somites spined dorsally, somites 4 and 5 with large lateral spines; telson deeply bifurcate, furcae heavily armed; setal formula I + ii + 3-7 (based on first stage zoeae). Presumably four or five larval stages.

Galathea (Sars 1889; Lebour 1930, 1931)

Rostrum acute, often expanded at base, may be armed distally; carapace posterolateral margin usually spinulate or denticulate, posterior spine rarely exceeding third abdominal somite; antennal scaphocerite broad, flattened, basal segment with single spine ventrally in stage I, two spines in all other stages; posterodorsal margins of abdominal somites minutely denticulate, but may become unarmed in later stages; distinct posterolateral spines on somites 4, 5, or both but may be absent later; no median dorsal spine on somite 6; telson triangular, not deeply bifurcate in early stages, becoming more elongate and truncately triangular in later stages; lateral spines may be denticulate; marginal setal formula in stages I and II of I + ii + 3-7, 3-8, respectively, and in all later stages I + ii + 3 + IV + 5-8. Four or five larval stages, pleopods present in last stage, as primordia in penultimate stage on occasion.

Munida (Sars 1889; Lebour 1930, 1931; Rayner 1935)

Rostrum elongate, needlelike, spinulate on dis-

tolateral margins and tips in early stages, but may be unarmed in later stages; a serrated posterolateral carapace margin with noticeable posterior spine, latter often extending to about fourth abdominal somite; antennal scaphocerite elongate, thin or even noticeably aciculate, often spined; basal segment with a single ventral spine in first stage, 2 in later stages; abdominal somites 2-5 with two or more spines or spinules dorsally, margin of somite 6 with a single larger median spine from stage III onward; telson originally deeply bifurcate in early stages of development, but becoming more triangularly truncate later, thus appearing similar to that in *Galathea* in later stages; telson furcae often spined; telson setal formula I + ii + 3-7, 3-7 or -8 in stages I and II and I + ii + 3 + IV + 5-9, 5-10, 5-11 or -12 in stages III-V, respectively. Four of five larval stages, pleopods present in last stage.

Munidopsis (Sars 1889; Samuelsen 1972)

Rostrum broad, flattened, nearly spatulate in all zoeal stages, profusely armed about outer margins; carapace with a large, forward-directed spine on anterolateral margin; entire ventral and posterolateral margins noticeably spinulate, posterior margin rounded, lacking elongate posterior spine otherwise typical of larvae in the family; antennal scaphocerite a flattened blade, two spines ventrally; posterodorsal margins of abdominal somites unarmed, a posterolateral spine present on somite 5; telson broadly spatulate, posterior marginal setal formula 1 + 2 + iii + IV + 5-15 in stage I, and I + 2 + iii + IV + 5-15 in stages II and III; other smaller hairs interspersed among setae 5-15. Three larval stages, pleopods present in each.

Pleuroncodes (Boyd 1960; Fagetti and Campodonico 1971)

Rostrum flattened basally, expanded similarly to that of *Galathea*, distal portion acute, margins noticeably spinulate, especially at tip; posterolateral carapace margins serrated, elongate posterior spines usually extending to fourth abdominal somite; antennal scaphocerite narrow, not as aciculate as in some *Munida*, basal segment with either 1 or 2 ventral spines; abdominal somites 1-5 heavily spined dorsally on posterior margins, becoming somewhat reduced in spination in later stages; somite 6 with a median dorsal spine in stage III and later; telson deeply bifurcate in stages I and II, becoming more truncately triangular in later stages as in *Munida* and *Galathea*; furcae may be denticulate; marginal setal formula I + ii + 3-7, 3-8 in stages I and II, and I + ii + 3 + IV + 5-9, 5-10, and 5-12 in stages III-V, respectively. Five larval stages, including up to eight substages in stage IV; stage VI in laboratory culture; pleopods present in stage V. The genus is presently restricted to the eastern Pacific Ocean.

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A THEORETICAL EXAMINATION OF SOME ASPECTS OF THE INTERACTION BETWEEN LONGLINE AND SURFACE FISHERIES FOR YELLOWFIN TUNA, *THUNNUS ALBACARES*

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ABSTRACT

This paper explores several aspects of a dual fishery (surface and longline) on yellowfin tuna, *Thunnus albacares*. The work is exploratory in nature and results, though indicative, are not conclusive for any specific fishery. Our results indicate that the yield per recruit is higher for the longline fishery than for surface gear if all fish are available to both gears and higher for the combined gears than for either gear fishing alone. The effect of fishing by one gear on yield to the other gear and the effect of the fishery on stock fecundity is shown to be greater for the often assumed 1:1 sex ratio than for the ratios usually observed. A simulation model was used to examine the interrelations of pattern of movement of fish, pattern of recruitment, and fishing strategy. It was assumed that movements were random and recruitment occurred either only along the coast or throughout the fishing area. The results indicated that either of these patterns of recruitment could allow for increased catch as the surface fleet moved offshore. However, location or pattern of recruitment is shown to be important when measuring natural mortality and for examining the potential of a localized fishery, primarily on younger fish, relative to a fishery exploiting the full range of the stocks or to one taking primarily older fish. Tagging and fecundity studies are suggested for further investigation of the questions examined in this paper.

An unsolved problem common to many of the tuna fisheries of the world is the nature of the interaction between longline and surface (i.e., seining, pole and line, and occasionally trolling and shallow handline) fisheries for the same species. Fisheries for yellowfin tuna, *Thunnus albacares;* albacore, *T. alalunga;* bluefin tuna, *T. thynnus;* southern bluefin tuna, *T. maccoyii;* and bigeye tuna, *T. obesus*, are prosecuted by both types of gear in the Pacific, Atlantic, and Indian Oceans. Although there can be considerable overlap of sizes of fish taken by the two types of gear, in general, longline gear takes larger (older) fish. Exploitation of a tuna stock by the two types of gear presents management with the problems of determining the effect of various combinations of fishing effort by the two gears on both yield per recruit to the two gears and recruitment to the stocks. In order to make these determinations, it is necessary to estimate 1) availability of the stock at each age to each of the two gears [The available portion of the stock is subject to both other mortality (any mortality not caused by gear of concern) and fishing mortality caused by the gear of concern. The unavailable portion of the stock is subject only to other mortality.], 2) fishing mortality of the available portion of the stock caused by each gear, 3) natural mortality, 4) growth, 5) fecundity, and 6) the relationship between egg production and recruitment.

The aim of this paper is to examine the interactions between longline and surface fisheries for yellowfin tuna and to determine the impact such interactions may have on the assumptions often made in assessment of yellowfin tuna fisheries and thus on the assessment calculations themselves. The paper is divided into three major sections. The first section examines the relationship between availability of the stock(s) of yellowfin tuna to surface and longline fishing and yield per recruit to the two gears. This is an important, and to our knowledge unexamined, aspect of all tuna fisheries exploited by both types of gear; the subsequent sections examine two asepcts of the biology of tuna that can affect the catch by each type of gear. The second section examines the effect of age specific sex ratios of yellowfin tuna on yield per recruit to the two types of gear and on egg production. The third section examines the effect of

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random migration or dispersal and location of recruitment of yellowfin tuna on estimates of mortality and yield per recruit to each gear. We have restricted our analysis to yellowfin tuna but believe that the concepts that we develop apply to the other species as well.

MATERIALS AND METHODS

While stocks of yellowfin tuna are subjects of important fisheries in all tropical oceans, information on vital parameters is sketchy and nonuniform. For example, tagging information available in the Pacific is lacking for the Atlantic stocks. On the other hand, regulation of the Pacific fishery makes interpretation of the catch information more difficult. Hence it is necessary to pick and choose from the available information that which is most relevant to the problems at hand. Although the parameters are likely to differ for fish from different oceans, if not fish from different areas of the same ocean, few studies have conclusively demonstrated that such differences exist. In addition, several (e.g., Lenarz et al. 1974) have found that conclusions from studies such as described in this paper are often insensitive to the likely range of values of parameters such as natural mortality, fishing mortality, and growth. In the first and second sections, we have used data primarily from the eastern Atlantic because historically catches have been more equally shared by longline and surface fisheries than in the eastern Pacific; in the third section we have modelled the eastern Pacific since information on migration patterns is more extensive. In both instances, the results are intended to be general rather than specific. Data extracted from one area and used in another is thought to be the best available and the question of real differences is left for further investigation.

With a noted exception, the growth equation $L = 194.8 \times (1 - e^{-0.42(t-0.67)})$ estimated by Le Guen and Sakagawa (1973) and length-weight equation $W = 0.0000214L^{2.9736}$ estimated by Lenarz (1974) are used for yellowfin tuna where L is fork length in centimeters, t is age in years, and W is weight in kilograms. Unless otherwise stated, we assumed that the annual instantaneous coefficient of natural mortality (M) is 0.8 (Hennemuth 1961). We estimated age-specific fecundity from two indices derived by Hayasi et al. (1972) (Table 1). Their index I was obtained from longline data and their index II was obtained from surface data. The fecundity indices were calculated by Hayasi et al. (1972) for fish caught in the Pacific by multiplying mean ova counts by percentage of mature female fish for each age and then dividing each product by the product calculated for age 3 fish. For much of our work, we used estimates of the 1967-71 average size (age) composition of the Atlantic yellowfin tuna fishery made by Lenarz et al. (1974) (Table 2). Use of length-age key assumes that length and age are equivalent. Sex composition shown in Table 2 is based on data from the Pacific.

TABLE 1.—Indices of fecundity of yellowfin tuna as interpolated from Hayasi et al. (1972), for fish caught in the Pacific calculated by multiplying average ova counts by percentage of mature female fish for each age and then dividing each product by the product calculated for age 3 fish.

Midpoint of size interval (cm)	Fecundity index I	Fecundity index II
80	0.04	0.07
85	0.04	0.14
90	0.05	0.21
95	0.08	0.27
100	0.15	0.36
105	0.23	0.42
110	0.33	0.51
115	0.42	0.61
120	0.55	0.70
125	0.70	0.81
130	0.88	0.92
135	1.12	1.04
140	1.40	1.15
145	1.80	1.26
150	2.30	1.37
155	2.77	1.50
160	3.20	1.62
165	3.57	1.76
170	4.05	1.91
175	4.42	2.06
180	4.82	2.23
	5.01	2.43

Estimates of the size- (age-) specific instantaneous coefficient of fishing mortality (F_t) on an annual basis were made using the Gulland (1965) and Murphy (1965) method. The computer program COHORT, written by W. W. Fox, Jr., of the Southwest Fisheries Center, was used to obtain estimates of F_t for each 5-cm size interval, beginning at 32.5 cm. The estimation procedure was initiated with a trial value of F_t for the largest size interval (Input F).

Estimates of F_t were obtained from the average 1967-71 catch composition data (Table 2) as was done by Lenarz et al. (1974). When feasible it is more desirable to estimate F_t from individual cohorts. This was not done because of the small number of years in the data series and belief that estimates from the average composition would adequately reflect conditions of the fishery. In a latter study, Fonteneau and Lenarz (1974) estimated F_t for individual cohorts from a longer time

TABLE 2.—Composite catch in numbers of yellowfin tuna by gear, sex, and size. Length composition by gear is based on data from Lenarz et al. (1974) on the Atlantic fishery. Sex composition is based on data from the Pacific (Murphy and Shomura 1972).

Age at beginning of interval (yr)	Midpoint of size interval (cm)	Male			Female		
		Surface	Longline	Total	Surface	Longline	Total
1.0579	35	1,179	0	1,179	1,179	0	1,179
1.1325	40	14,528	0	14,528	14,528	0	14,528
1.2039	45	61,563	0	61,563	61,563	0	61,563
1.2888	50	186,611	4	186,615	186,611	4	186,615
1.3710	55	237,622	11	237,633	237,622	11	237,633
1.4562	60	210,711	226	210,937	210,711	226	210,937
1.5445	65	121,824	324	122,148	121,824	324	122,148
1.6363	70	137,389	1,076	138,465	137,389	1,076	138,465
1.7317	75	102,046	2,718	104,764	102,046	2,718	104,764
1.8310	80	90,710	2,847	93,557	90,710	3,847	93,557
1.9348	85	67,060	6,013	73,073	67,060	6,013	73,073
2.0432	90	52,541	6,525	59,066	52,541	6,525	59,066
2.1568	95	51,366	5,833	57,199	51,366	5,833	57,199
2.2761	100	56,714	7,537	64,251	56,714	7,537	64,251
2.4017	105	52,752	17,036	69,788	52,752	17,036	69,788
2.5343	110	51,497	20,105	71,602	51,497	20,105	71,602
2.6748	115	35,981	22,017	57,998	35,981	22,017	57,998
2.8240	120	26,167	21,430	47,597	26,167	21,480	47,597
2.9832	125	30,779	28,679	59,458	30,779	28,679	59,458
3.1538	130	26,001	29,272	55,273	26,001	29,272	55,273
3.3376	135	21,975	22,345	44,320	21,975	22,345	44,320
3.5368	140	16,749	26,035	42,784	16,749	26,035	42,784
3.7542	145	26,919	38,782	65,701	11,661	16,800	28,461
3.9935	150	31,942	36,099	68,041	8,450	9,549	17,999
4.2595	155	24,727	33,933	58,665	3,767	5,170	8,937
4.5590	160	18,701	22,644	41,345	1,524	1,845	3,369
4.9017	165	14,497	13,140	27,637	573	519	1,092
5.3021	170	5,621	6,162	11,783	94	103	197
5.7838	175	3,703	240	3,943	21	1	22
6.3883	180	1,836	55	1,891	3	0	3
Total		1,781,711	371,093	2,152,804	1,679,858	254,020	1,933,878

span and obtained results similar to Lenarz et al. (1974).

The computer program MGEAR, written by W. H. Lenarz, was used to obtain estimates of yield per recruit using the Ricker (1958) yield equation. A description and listing of MGEAR is available from its author. The program was slightly modified to calculate indices of egg production using the following equation

$$E_{t_1,t_2} = 0.5\,(t_2 - t_1)\,N_{t_1}\,(FI_{t_1} + FI_{t_2}e^{-(F_{t_1} + M_{t_1})(t_2 - t_1)})$$

where E_{t_1,t_2} = index of egg production between age t_1 and t_2,
FI_{t_1} = index of fecundity for age t_1,
N_{t_1} = number of females in population of age t_1,
F_{t_1} = coefficient of instantaneous fishing mortality between age t_1 and age t_2, and
M_{t_1} = coefficient of instantaneous natural mortality between age t_1 and age t_2.

For this equation it is assumed that the estimates of FI are proportional to egg production per female, which is assumed to be continuous, and that the rate of egg production is linear over the interval (t_1, t_2).

A computer program MIGR was written by J. R. Zweifel to perform the calculations used for the third section of this paper. Since new methodology is developed, a description of the calculations will be given in that section.

AVAILABILITY OF THE STOCK(S) OF ATLANTIC YELLOWFIN TUNA TO SURFACE AND LONGLINE GEAR

In previous works on yield per recruit, yellowfin tuna of all ages in either the entire Atlantic (e.g., Hayasi and Kikawa 1970; Wise 1972; Hayasi et al. 1972; Lenarz et al. 1974), or in the eastern Atlantic (e.g., Fonteneau and Lenarz 1974) were assumed to be equally available to both longline and surface gear. However, since the surface fishery for yellowfin tuna occurs very close to the west African coast (Fox and Lenarz 1973) while the longline fishery for yellowfin tuna is distributed throughout the tropical Atlantic, it seems possible that the longline fishery is exploiting some fish that are not available to the surface fishery. It is

also possible that some stock(s) which are available to surface fishing are never available to the longline fishery. Since significant tagging efforts have begun only recently in the Atlantic and the results of these studies have not been published, data are not available to evaluate the availability of yellowfin tuna to both gears.

However, there is evidence from the Pacific that yellowfin tuna are not equally available to longline and surface gears. With the permission of W. H. Bayliff of the Inter-American Tropical Tuna Commission (IATTC), we examined yellowfin tuna tag return data from the eastern Pacific during 1963-66 in an attempt to evaluate the availability of fish to both gears in that area. We tabulated the number of tag returns for fish larger than 100 cm at return by 10-cm size groups (Table 3). All of the fish had been at liberty for at least 10 mo. Although all of the tagged fish were measured when released, not all were measured when recovered. Bayliff recommended the relationship

$$L = 167\,(1 - e^{-0.6(t-0.833)})$$

estimated by Davidoff (1963) for growth of yellowfin tuna in the eastern Pacific as the best equation to estimate the size of unmeasured fish. All of the returns were surface-caught fish, even though longliners captured a considerable number of yellowfin tuna in the eastern Pacific (east of long. 130°W) (Kume and Joseph 1969). In fact for many of the 10-cm size groups, the longliners caught more yellowfin tuna than the surface gear operators (Table 4).

TABLE 3.—Number of returns of tagged yellowfin tuna from the eastern Pacific Ocean by size interval and year (W. H. Bayliff, pers. commun.).

Size interval (cm)	1963	1964	1965	1966
101-110	2	16	3	3
111-120	1	7	1	1
121-130	2	0	2	0
131-140	0	0	0	1
141-150	0	0	0	0
151-160	0	0	1	0

Again at the suggestion of Bayliff, we estimated the expected return of tags from longline-caught fish when all fish are equally available to both gears. Assuming tag recoveries were independent of each other, recovered tags were reported at the same rate by both components of the fishery, and tagged fish were equally available to both gears: then the expected returns of tagged fish of size i by gear j in year k is given by

$$E(R_{ijk}) = R_{i\cdot k} N_{ijk} / N_{i\cdot k} \qquad (1)$$

$$i = \begin{cases} 1, \text{ when size is between 101 and 110 cm} \\ . \\ . \\ . \\ 6, \text{ when size is between 151 and 160} \end{cases}$$

$$j = \begin{cases} 1, \text{ when fish are caught by surface gear} \\ 2, \text{ when fish are caught by longline gear} \end{cases}$$

$$k = \begin{cases} 1, \text{ when fish are caught in 1963} \\ 2, \text{ when fish are caught in 1964} \\ 3, \text{ when fish are caught in 1965} \\ 4, \text{ when fish are caught in 1966} \end{cases}$$

where R_{ijk} = number of returns and
N_{ijk} = number of fish caught.

A dot in the position of a subscript signifies summation of the variable over the subscript, e.g., $X_{i\cdot k} = \sum_{j=1}^{2} X_{ijk}$.

Forty fish were returned by the surface gear during 1963-66 (Table 3). Using the statistics of Tables 3 and 4 and the three assumptions, a return of 5.4 of these tags would have been expected from the longline fishery and 34.6 from the surface fishery. The chi-square value, corrected for discontinuity, for the observed and expected returns (Equation 1) is 5.13, with probability slightly less than 0.025. The power of the test of the hypothesis of independence, equal reporting rate, and equal availability was reduced because we combined the year and size strata to avoid

TABLE 4.—Catch of yellowfin tuna from the eastern Pacific Ocean (east of long. 130°W) in hundreds of fish by size and gear (Kume and Joseph 1969).

Size interval (cm)	1963		1964		1965		1966	
	Surface gear	Longline gear	Surface gear	Longline gear	Surface gear	Longline gear	Surface gear	Longline gear
101-110	653	336	4,082	173	3,386	30	2,926	54
111-120	473	455	2,245	465	2,211	93	2,044	116
121-130	508	390	720	1,078	1,895	444	1,312	304
131-140	237	751	448	804	905	758	718	515
141-150	240	541	320	469	498	466	536	575
151-160	212	144	102	104	194	205	204	200

strata with low expected values. The probability under Equation (1) of a returned tag being from a surface-caught fish (P_{i1k}) is

$$P_{i1k} = N_{i1k}/N_{i\cdot k} \ . \qquad (2)$$

The exact probability of all returns during the 1963-66 period being from surface-caught fish, given the distribution of returns among year and size categories, is

$$P_{\cdot 1\cdot} = \prod_{i=1}^{6} \prod_{k=1}^{4} (P_{i1k})^{R_{i\cdot k}} \ . \qquad (3)$$

Our estimate of $P_{\cdot 1\cdot}$ is 0.00152, which is very low and indicates that Equation (1) does not hold. Thus we may conclude that 1) tag returns are not independent (e.g., fish that were captured from a school and tagged may remain in the same school until recaptured), and/or 2) longline recoveries are reported at lower rates than surface recoveries, and/or 3) the fish were not equally available to both gears. Since all fish were at liberty for more than 10 mo before being recovered, the assumption of tag returns being independent seems likely to be valid. The independence of tag returns would seem to be a desirable subject for further research since the assumption is so often made in analyses of tag returns. A considerable number of southern bluefin tuna have been recovered and returned by longliners (Shingu 1970), indicating longline fishermen do cooperate in tagging programs. During the period of the study, the surface fishery was only beginning to move offshore (Calkins and Chatwin 1971), while the longline fishery was distributed throughout the area (Kume and Joseph 1969). Also, the fish that were released were caught by surface gear, tagged, and released in nearshore areas. Thus, tagged fish were probably more representative of fish exploited by the surface fishery than those that were exploited by the longline fishery, if two groups of fish existed. Thus it seems plausible that the tagged fish were not equally available to longline and surface gears.

This is further evidence of unequal availability of yellowfin tuna to the two gears in the Pacific. Previously, Hisada (1973) showed that yellowfin tuna caught near the surface using handlines were of the same size as those caught by longliners at the same time and in the same area of the western Pacific. However, the surface-caught fish tended to be more sexually mature except in areas in which the 26°C isotherm occurred at depths fished by longliners. He attributed this phenomenon to a preference for warmer waters by sexually mature fish and noted that larvae of yellowfin tuna tend to be found at water temperatures exceeding 26°C. Thus, some yellowfin tuna evidently behave in a fashion that makes them available to surface fishing but not to longline fishing. Further evidence along these lines is provided by Shingu and Tomlinson (Patrick K. Tomlinson, Inter-American Tropical Tuna Commission, La Jolla, Calif. Pers. commun., 1974) who found that the length-weight relationship estimated by Lenarz (1974) for surface-caught yellowfin tuna in the Atlantic was more representative of the longline catch in the eastern Pacific than was the relationship estimated by Chatwin (1959) for surface-caught yellowfin tuna in the eastern Pacific.

With the above in mind, we considered three hypothetical stock structures for the Atlantic yellowfin tuna fishery: 1) the same stock(s) are equally available to both gears, 2) half of the catch of the longline fishery comes from stock(s) not available to the surface fishery, and 3) the entire catch of the longline fishery comes from stock(s) not available to the surface fishery. The effects of the three hypotheses on estimates of fishing mortality and yield per recruit to the gear were examined.

Using the data in Table 2, we estimated the vector F of size-specific instantaneous mortality rates F_t under the three hypotheses which are identified by the proportion ϕ of the longline catch which comes from the stocks exploited by the surface fishery as $\phi = 1.0$, 0.5, and 0.0 respectively. For $\phi = 1.0$, all of the data in Table 2 was used to estimate the F vector. For $\phi = 0.5$, the surface catch plus 50% of the longline catch was used and for $\phi = 0.0$ only the surface catch was used for estimating F. When $\phi = 0$, an additional F vector was estimated for a longline fishery operating without the presence of a surface fishery by using only the longline catch. The F vectors were then used to calculate yield per recruit to the two gears. Estimation of a vector of size-specific F requires an estimate of natural mortality and size-specific F for one size category. In all instances, we chose to use an estimate of size-specific F for the fish >177.5 cm. This estimate will be referred to as Input F. The final value of size-specific F was set at 0.2 following Lenarz et al. (1974). The estimates (Figure 1) indicate that values of F for large fish are directly related to the portion of the longline catch that comes from the stock(s) exploited by the

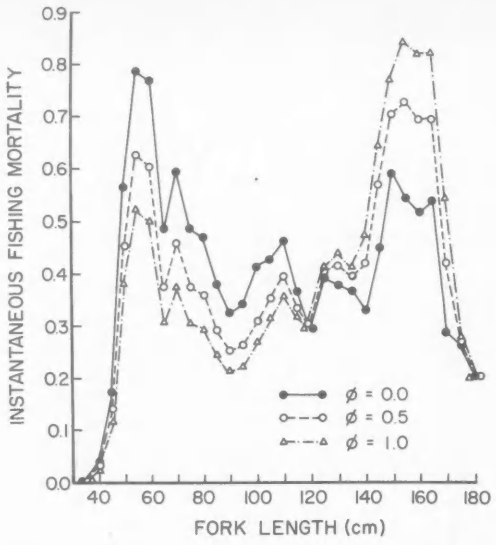


FIGURE 1.—Estimates of size-specific fishing mortality of Atlantic yellowfin tuna as a function of porportion of catch (ϕ) by longline fishery that comes from stock(s) exploited by surface fishery.

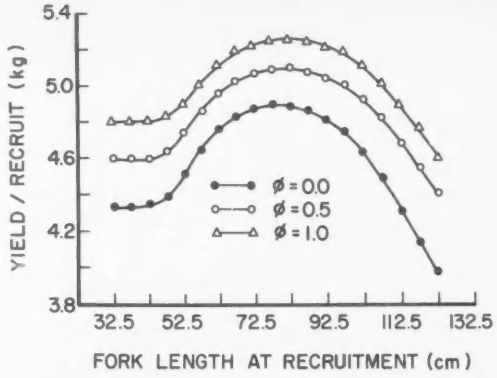


FIGURE 2.—Yield per recruit (kilograms) of Atlantic yellowfin to surface and longline gear as a function of size at recruitment and proportion of catch (ϕ) by the longline fishery that comes from stock(s) exploited by surface fishery. The vector of fishing mortality is equal to the value at the time of study.

surface fishery. The relative values of yield per recruit within a hypothesis are not significantly affected by the portion of the longline catch that comes from the stock(s) exploited by the surface fishery (Figure 2). Therefore, the three hypothetical stock structures do not seem to have much bearing on decisions concerning minimum size regulations.

Estimates of yield per recruit were also plotted as functions of fishing effort (mortality), size at recruitment, and portion of longline catch that comes from stock(s) exploited by the surface fishery. Again the relative values of the results are not significantly influenced by the stock structure (Figure 3a, b). We note that Figure 3 is in agreement with the conclusion of Fox and Lenarz (1974), "... that the Atlantic yellowfin fishery is approaching or has obtained a plateau where substantially increased sustainable average yield of yellowfin tuna will not be obtained by increasing fishing effort without some concomitant change in the constitution of the fishery. ..." They used the production model approach under the alternative assumptions that either the longline or surface gear exploits the same or separate stock(s).

The effect of the surface fishery on the longline fishery was examined by estimating yield per recruit to the longline fishery in the presence and in the absence of a surface fishery (Figure 4). The results suggest that if the two gears exploit the same stock(s), the surface fishery reduces the potential yield per recruit to the longline fishery by about twofold at the position of the fishery during the study period (i.e., multiplier of effort = 1) and about fivefold for a threefold increase in effort. The same procedure was used to examine the effect of the longline fishery on the surface fishery (Figure 5). The results indicate that at the level of fishing effort at the time of study, the yield per recruit to the surface fishery would be increased by 25% if the longline fishery ceased.

Although the presence of each fishery reduces the yield per recruit of the other, the yield per

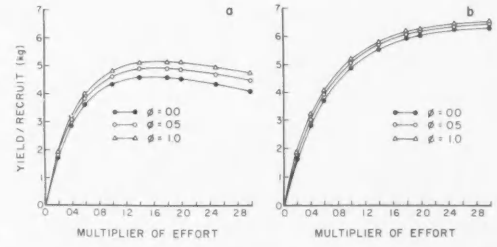


FIGURE 3.—Yield per recruit of Atlantic yellowfin tuna as a function of fishing effort and proportion of catch (ϕ) by longline fishery that comes from stock(s) exploited by surface fishery: (a) size at recruitment is 32.5 cm, (b) size at recruitment is 77 cm.

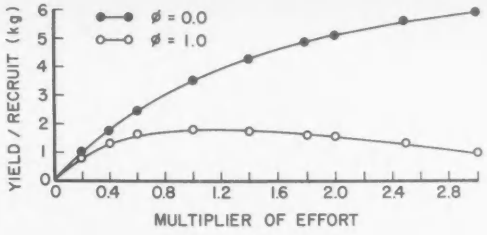


FIGURE 4.—Estimates of yield per recruit of Atlantic yellowfin tuna to the longline fishery as a function of effort and presence (ϕ = 1.0) or absence (ϕ = 0.0) of a surface fishery.

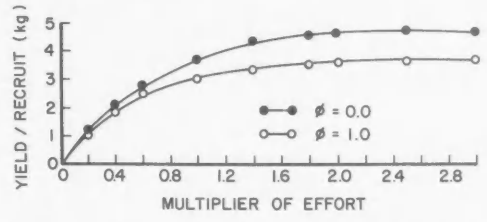


FIGURE 5.—Estimates of yield per recruit of Atlantic yellowfin tuna to the surface fishery as a function of effort and presence (ϕ = 1.0) or absence (ϕ = 0.0) of longline fishery.

recruit of the combined fisheries is higher than the yield per recruit of either fishery alone. The results suggest that if a catch quota system is imposed on the Atlantic yellowfin tuna fishery, all components should be included unless it is shown that different stock(s) are being exploited by the gear.

The above results (Figures 4, 5) suggest that a stock of yellowfin tuna will produce a potentially higher yield per recruit to a longline fishery than to a surface fishery, if the fish are equally available to the two gears. However, until the question of availability is settled, it is not possible to predict the potential production to the two gears. We point out here that gear-specific availability is not well known for any tuna fishery and would be difficult to determine. Thus, we are faced with the prospect of probably being forced to determine empirically the production potential for each gear in each fishery. After a fishery is established, an analysis of the type conducted on the Atlantic yellowfin tuna fishery could be used to examine the effects of availability to the two gear types, and a tagging study could be designed to provide the required answers.

EFFECTS OF AGE-SPECIFIC SEX RATIOS OF ATLANTIC YELLOWFIN TUNA ON YIELD PER RECRUIT TO THE TWO TYPES OF GEAR AND STOCK FECUNDITY

While a number of authors have noted that the ratio of females to males appears to be less than 1:1 for catches of larger tunas, none to our knowledge has incorporated these observations into calculations of yield per recruit or stock fecundity. Beardsley (1971) reported that the ratio of female to male Atlantic longline-caught albacore was 233:365 during the December 1969-September 1970 period. Males increasingly dominated at sizes >100 cm. Females slightly outnumbered males between 92 and 100 cm. One explanation for the catch curves estimated by Beardsley is a 1:1 sex ratio at small sizes, a slightly slower growth for females for fish >90 cm, and beyond 100 cm, either a higher rate of natural mortality for females or a change in behavior that makes females less available than males to longline fishing. Other explanations exist, e.g., a combination of low sex ratio and slow growth of females throughout their life. Sakamoto (1969) noted for Atlantic bigeye tuna, ". . . males predominated in areas of higher water temperature. Proportion of females increase as the water temperature gets lower." His data indicate that as size increases the proportion of females decreases and females may grow slower than males in waters between lat. 30° to 50°N, but not in equatorial waters. Data presented by Kikawa (1964) indicate that southern bluefin tuna >150 cm are predominantly males, while females often outnumber males at smaller sizes. Thus, female southern bluefin tuna may grow more slowly than males.

Since there is considerable evidence for age-specific changes in the sex ratio of tunas, we believe that the effects of such changes on estimates of yield per recruit to each gear type and fecundity should be investigated. We have assumed sex ratios to be the same as with Pacific yellowfin tuna because no extensive studies of age-specific sex ratios for Atlantic yellowfin tuna have been published. We used results from a study by Murphy and Shomura (1972), who found that beyond 140 cm male yellowfin tuna greatly outnumbered females (Figure 6). The data in Figure 6 do not show a large excess of females in any size interval and thus no evidence of sex-specific growth is exhibited. Using their data and the age-length

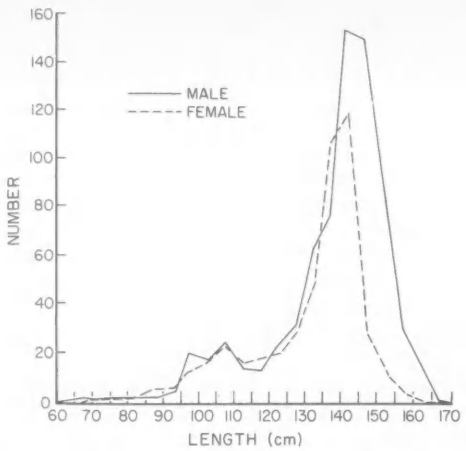


FIGURE 6.—Length distribution by sex of longline-caught yellowfin tuna in the central Pacific Ocean (Murphy and Shomura 1972).

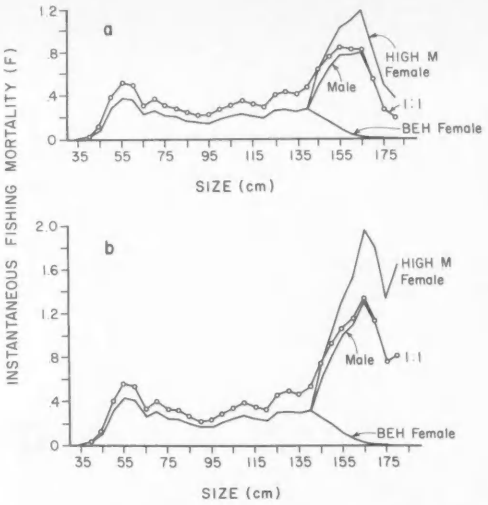


FIGURE 7.—Estimates of size and sex specific coefficient of instantaneous fishing mortality on annual basis (F) for Atlantic yellowfin tuna for 1:1, BEH and HIGH M hypotheses (see text): (a) low Input F, B) high Input F.

relationship of LeGuen and Sakagawa (1973), we estimated that beyond 140 cm

$$\ln R = 6.74 - 1.96t \qquad (4)$$

where R = ratio of females to males
t = age in years.

One interpretation of the above result (assuming that males have a coefficient of instantaneous natural mortality of 0.8 on an annual basis as do all fish <145 cm) is that female yellowfin tuna >140 cm have a coefficient of apparent natural mortality of 2.76. Assuming that the results of Murphy and Shomura apply to the Atlantic and that all yellowfin tuna are equally available to both gears, we separated the catch of yellowfin tuna into males and females using Equation (4) and Table 2, and estimated F for the males using Input F values of 0.2 and 0.8 for fish >177.5 cm (Lenarz et al. 1974). An alternative method would be to use the same Input F for the three hypotheses at the smallest size interval. This was attempted and resulted in either estimates of F_t which, based on the results of other studies, appeared to be too low under the 1:1 hypothesis or too high under the other hypotheses. The estimates of size-specific F are similar except for very large yellowfin tuna (Figure 7). Since the deviations in sex ratio from 1:1 occurs only at large sizes, we used both sets of estimates of F.

For females, three hypotheses were examined for estimating F: 1) the observed differences in sex ratios are artifacts, and consequently females have the same values of F and M as males (denoted 1:1); 2) females >140 cm have a higher natural mortality rate than males but are exploited at the same rate as males for all sizes (denoted as HIGH M); and 3) females have the same natural mortality rate as males but become less subject to fishing mortality beyond 140 cm (denoted as BEH for behavior changes). Under the BEH hypothesis, F_t for females >140 cm is equal to the ratio of the catch of females to the catch of males times F_t estimated for males. The alternative hypotheses considerably affected the estimates of size-specific F (Figure 7).

In the following analyses, we found that the BEH and HIGH M hypotheses produce similar results. To save space, we refer to only the one hypothesis that produced results which showed the greatest difference from the 1:1 hypothesis. Also, when not specifically indicated, size of recruitment and effort are assumed to be those at the time of the study, i.e., 1967-71 where the multiplier of effort is equal to unity.

Estimates of yield per recruit as a function of fishing effort are shown in Figure 8. The choice of Input F has little effect on the relative values of

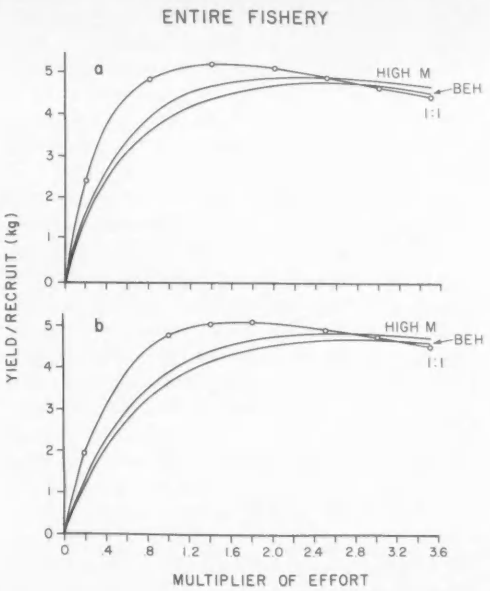


FIGURE 8.—Estimates of yield per recruit of Atlantic yellowfin tuna at size of recruitment at time of the study as a function of fishing effort and sex hypothesis: (a) high Input *F*, (b) low Input *F*.

yield per recruit. Yield per recruit is closer to the maximum under high Input *F* than low Input *F*. The curves are considerably more dome-shaped when a 1:1 sex ratio is assumed than under the other two hypotheses. Under high Input *F* and the 1:1 hypothesis only a 3% increase in yield per recruit could be obtained by increasing fishing effort. Under the BEH hypothesis, a 20% increase in yield per recruit could be obtained by doubling the effort.

Estimates of yield per recruit as a function of size at recruitment are shown in Figure 9. Again the choice of Input *F* has little effect on the relative values of yield per recruit. A slightly greater dependence of yield per recruit on minimum size is obtained when the high Input *F* is used. Under high Input *F*, and the 1:1 hypothesis a 10% increase in yield per recruit could be achieved by increasing size at recruitment. Under the BEH hypothesis, only a 5% increase would occur. Eumetric fishing occurs when size at recruitment is raised from the current 32.5 to 82.5 cm under the 1:1 hypothesis and 72.5 cm under the BEH hypothesis.

Estimates of yield per recruit as a function of fishing effort were also calculated for each gear

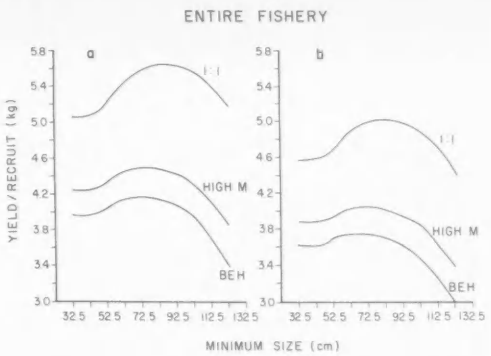


FIGURE 9.—Estimates of yield per recruit of Atlantic yellowfin tuna at level of fishing effort at the time of the study for 1:1, BEH and HIGH *M* hypotheses as a function of size at recruitment: (a) high Input *F*, (b) low Input *F*.

(Figure 10). The results show that the curves are more dome-shaped for the longline fishery than for the surface fishery under all three hypotheses. Furthermore, the longline fishery is more sensitive to fishing effort under the 1:1 hypothesis than under the other two. The curves for the surface fishery are dome shaped under the 1:1 hypothesis, but appear to approach an asymptote under the other two.

We also estimated yield per recruit for each gear when the other gear is not exploiting the stock (Figure 11). A comparison of Figures 10 and 11 reveals that yield per recruit to the longline fishery would increase by about 115% if surface fishing were eliminated under high Input *F* and the 1:1 hypothesis and 76% under high Input *F* and the BEH hypothesis. Yield per recruit to the surface fishery would increase by about 30% if the longline fishery were eliminated under high Input *F* and the 1:1 hypothesis and 22% under the BEH hypothesis. Thus, the nature of age-specific sex ratio has a greater effect on that of the longline fishery than on the relative success of the surface fishery. The curves for a longline fishery in the presence of a surface fishery are dome-shaped (Figure 10), while the curves in the absence of a surface fishery are not (Figure 11). This again points out the importance of not treating the two fisheries as separate entities unless it is shown that they exploit separate stocks.

Stock fecundity (egg production per recruit) relative to an unfished stock was estimated as a function of fishing effort. Stock fecundity was considerably affected by the choice of fecundity index

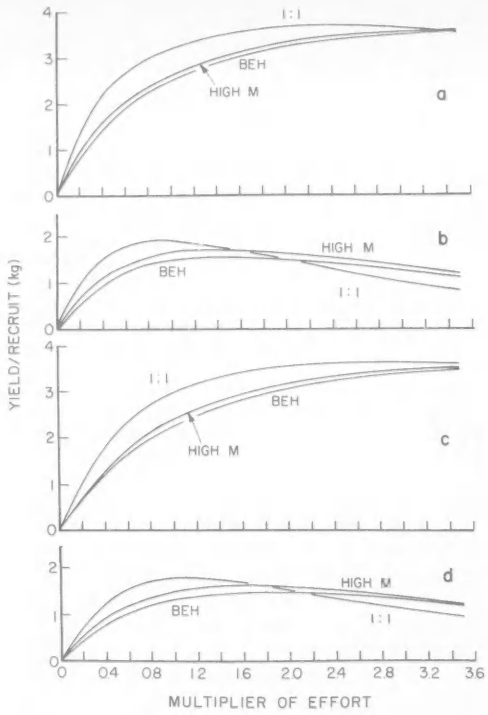


FIGURE 10.—Estimates of yield per recruit of Atlantic yellowfin tuna when both gear fish at size of recruitment at the time of the study as a function of sex ratio hypothesis, fishing effort, and gear: (a) surface gear with high Input F, (b) longline gear with high Input F, (c) surface gear with low Input F, and (d) longline gear with low Input F.

and sex ratio hypothesis but only slightly affected by the choice of Input F (Figure 12). At the level of fishing effort at the time of the study under high Input F and 1:1 hypotheses, the relative fecundity is 0.28 when the fecundity index I is used and 0.39 when fecundity index II is used. Under the HIGH M hypothesis, relative fecundity is 0.55 when fecundity index I is used and 0.61 when fecundity index II is used. Thus, at the level of fishing effort at the time of the study, the choice of fecundity has a 10 to 30% effect on estimates of relative fecundity, while the choice of sex ratio hypothesis has a 30 to 50% effect. The two choices, fecundity index and sex ratio hypothesis, also have considerable effect on relative fecundity when plotted as a function of size at recruitment (Figure 13).

The relationship between stock fecundity and recruitment has not been demonstrated for any tuna. As shown above, one of the difficulties in demonstrating such a relationship is obtaining a reasonably accurate estimate of stock fecundity. Even if stock fecundity could be accurately determined, the recruitment process is likely to be so complex that much more research would be required before a reliable predictor of recruitment could be developed.

It is interesting to note that similar estimates of yield per recruit and relative fecundity are obtained under the HIGH M and BEH hypotheses. Thus it appears that research should be directed toward determining whether or not the 1:1 hypothesis or one of the other two are valid rather than distinguishing between the HIGH M and BEH hypotheses. This research should be a fairly simple matter. The choice of fecundity index is also of significance for estimating relative fecundity. The difference between the two indices is caused mainly by different maturity schedules (Hayasi et al. 1972). The surface-caught fish appeared to mature at an earlier age than longline-caught fish, and could be an artifact related to the phenomenon noted by Hisada (1973); i.e., mature fish tend to prefer warm water. It should also be a fairly simple matter to determine the cause of the difference between the two indices.

SIMULATION MODEL OF PATTERNS OF DISPERSAL AND RECRUITMENT OF YELLOWFIN TUNA

Factors that could cause groups of tuna to not be available to all components of a fishery include nonrandom movements, random movements but nonrandom distribution of fishing gear or effort, and recruitment that is nonrandom in a geographical sense.

Extensive tagging experiments have not produced any clear-cut evidence of a definite migration pattern for yellowfin tuna in the eastern Pacific. Bayliff and Rothschild (1974) recently found evidence for both random dispersal and directed movements. They were not able to remove the effects on their data of lack of fishing effort in some time-area strata and of the coastal boundary. The evidence for directed movements indicated that such movements were generally parallel to the coast, suggesting that the presence of the coast influenced their results. Fink and Bayliff (1970), in a synthesis of extensive tagging data, proposed that recruitment to the nearshore surface fishery is not random in a geographical sense, but tends to take place off Mexico and in the Panama Bight.

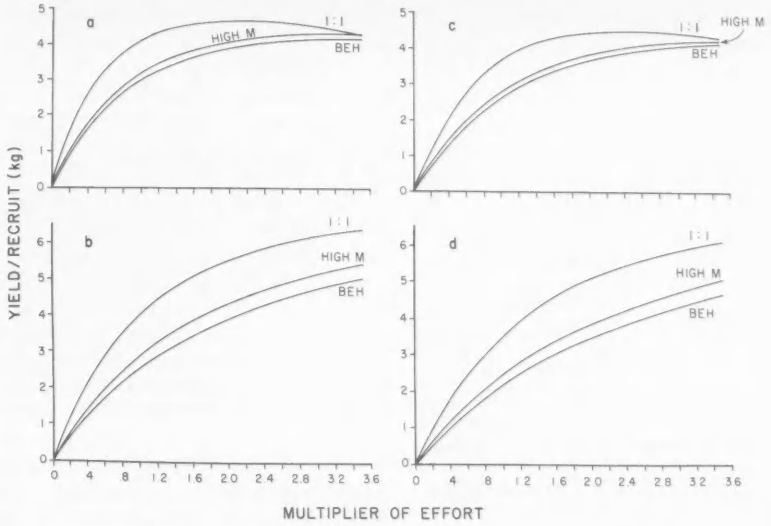


FIGURE 11.—Estimates of yield per recruit at size at recruitment at the time of the study as a function of fishing effort, sex ratio hypothesis, and fishing gear when only one gear is fishing: (a) high Input F and surface gear, (b) high Input F and longline gear, (c) low Input F and surface gear, and (d) low Input F and longline gear.

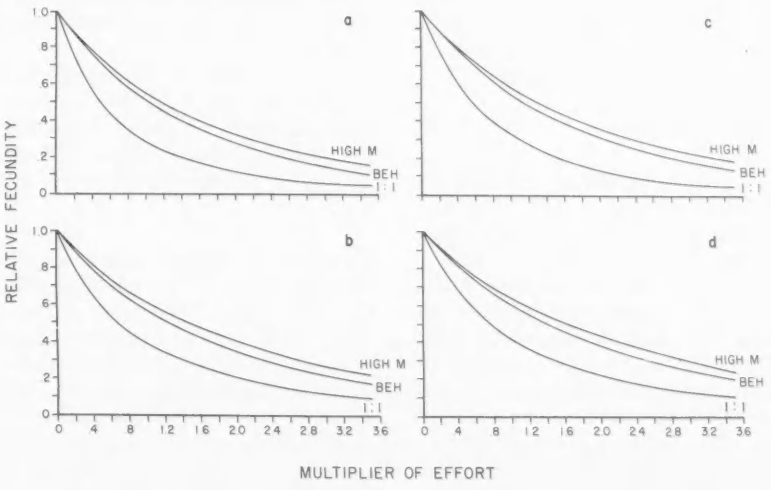


FIGURE 12.—Estimates of relative stock fecundity at size at recruitment at the time of the study as a function of fishing effort, fecundity index, and sex ratio hypothesis: (a) high Input F and fecundity index I, (b) high Input F and fecundity Index II, (c) low Input F and fecundity index I, and (d) low input F and fecundity index II.

With the above results in mind, we developed a computer simulation model to examine the interrelationships of: 1) patterns of movement of fish; 2) patterns of recruitment (i.e. by area), and 3) fishing strategy for two gear types (surface and longline) fishing alone or together on the same population.

The model is general in that it allows the user to

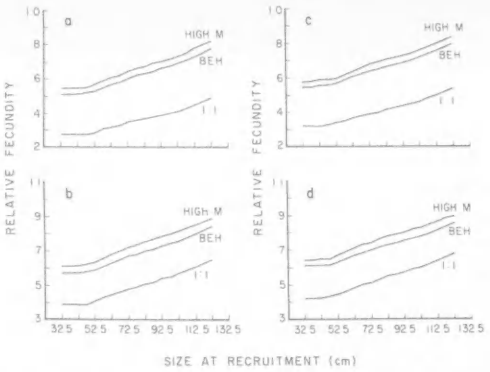


FIGURE 13.—Estimates of relative stock fecundity at level of fishing effort at the time of study as a function of size at recruitment, fecundity index, and sex ratio hypothesis: (a) high Input F and fecundity index I, (b) high Input F and fecundity index II, (c) low Input F and fecundity index I, and (d) low Input F and fecundity index II.

specify the nature of movements, locations of recruitment, parameters of growth, and natural fishing mortality.

We crudely represented the eastern Pacific Ocean with the grid of 5° square areas shown in Figure 14. The number of fish of a specific age in each cell at time t is given by the vector

$$N_t = AS_tN_{t-1} \tag{5}$$

where N_t (112 × 1) has elements $(n_i)_t$ equal to the number of fish in cell i at time t, S_t (112 × 112) is a diagonal matrix with elements $(s_{ii})_t$ equal to the survival rate of fish in cell i from time $t-1$ to time t, A(112 × 112) is a probability transfer matrix with elements (a_{ij}) equal to the probability of a fish in cell j moving to cell i, and where N_0(112 × 1) has elements $(n_i)_0$ equal to the number of recruits in cell i. Five consecutive year classes are in the system at a time.

For our work we specified A, the transfer matrix, by the assumption that for any cell the probabilities of fish remaining stationary and moving to each of eight adjacent cells is the same, i.e., 1/9. Any other transfer has zero probability. This general rule is modified as follows:

1) Probabilities of remaining stationary in cells adjacent to the shore are augmented by the sum of probabilities of those movements which would otherwise put fish on land and the probability of occurrence on land is zero.

COLUMN

ROW	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	1	2	3	4	5	6	7	8	9	10	11	12	13	14
2	15	16	17	18	19	20	21	22	23	24	25	26	27	28
3	29	30	31	32	33	34	35	36	37	38	39	40	41	42
4	43	44	45	46	47	48	49	50	51	52	53	54	55	56
5	57	58	59	60	61	62	63	64	65	66	67	68	69	70
6	71	72	73	74	75	76	77	78	79	80	81	82	83	84
7	85	86	87	88	89	90	91	92	93	94	95	96	97	98
8	99	100	101	102	103	104	105	106	107	108	109	110	111	112

FIGURE 14.—Representation of eastern Pacific Ocean. Each cell represents a 5° square area. Hatched cells represent land. Column 1 is western boundary and Column 14 is eastern boundary. Row 1 is northern boundary and row 8 is southern boundary.

2) Probabilities projecting beyond the northern and southern edges are similarly absorbed on the boundaries.

3) In cells of rows 2 and 7, probabilities of moving toward rows 1 and 8 are decreased by half with the probability of remaining stationary increased by a like amount. This is an attempt to simulate a stock encountering increasingly marginal conditions as the northern and southern boundaries are approached.

4) Probabilities of remaining stationary on the western edge are augmented by the probability of returning from beyond the boundary in a single time interval. The remainder of the fish that move beyond the western boundary are lost to the system.

The speed of dispersion is controlled both by A and the time interval. The time interval was 3 mo for this study. The combination of A as defined and time interval of 3 mo allows a fish to travel a maximum of 1,200 mi in a year. Only 1 out of 820 surviving fish that begin the year in the center of the grid travel 1,200 mi in a year. These relatively slow random movements seemed reasonable, based on the results shown in Bayliff and Rothschild (1974) and recent results of IATTC tagging studies (Inter-American Tropical Tuna Commission[3]).

Two alternative recruitment models were examined. For the first, denoted as inshore re-

[3]Cited with permission of M. Clifford Peterson, Acting Director of the Inter-American Tropical Tuna Commission. From the Inter-American Tropical Tuna Commission Bi-monthly Report, March-April 1976:8-13.

cruitment, recruits are divided equally among the five cells 51, 52, 69, 83, and 84, which resemble the recruitment areas proposed by Fink and Bayliff (1970). For the other alternative, denoted as uniform recruitment, recruits are divided equally among all cells except those on the boundaries or on land. Total annual recruitment is 100 fish. We assumed 1) that fish are 1 yr old when recruited, 2) growth proceeds according to the von Bertalanffy curve of LeGuen and Sakagawa (1973), and 3) the coefficient of instantaneous natural mortality is 0.8 on annual basis and is independent of time and location. Fish >6 yr old (175 cm) were removed from the system. Consequently, under constant conditions the fishery reaches equilibrium in 5 yr. The system was always run for 5 yr before an experiment was begun.

We first examined the effects of sampling location, dispersal, and location of recruitment on age distribution and the resulting apparent rate of natural mortality obtained from unbiased samples from an unfished population. Mortality was estimated with the standard linear regression model ($\ln N_t = \ln N_0 - Mt$) from the age distribution of fish in each cell. It is assumed that mortality is constant after full recruitment, and that the modal age represents first age of full recruitment. The results reveal that M is usually overestimated as would be expected when fish emmigrate from a sampled area (Figure 15). Estimates of M tend to be relatively high near areas of spawning with inshore recruitment. In the case of uniform recruitment, estimates of M tend to be highest on the western boundary where fish are lost to the system. Modal age tends to increase in a westerly direction for inshore recruitment and stay relatively constant for uniform recruitment (Figure 15). The modal size of actual catches of surface-caught yellowfin tuna in the eastern Pacific increases in a westerly direction (Figure 16). Although the surface fishery probably does not take an unbiased sample of the size distribution of the population, the data are suggestive of reduced recruitment in the western areas.

We simulated a 20-yr hypothetical yellowfin tuna fishery to examine interactions among a longline fishery, inshore surface fishery, ocean-wide surface fishery, and ocean-wide surface fishery that does not heavily exploit young fish as follows:

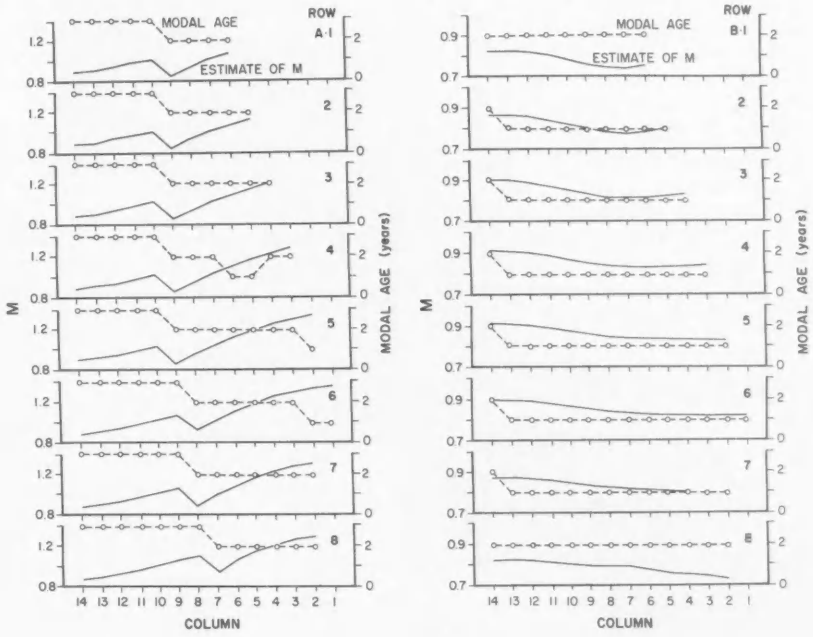
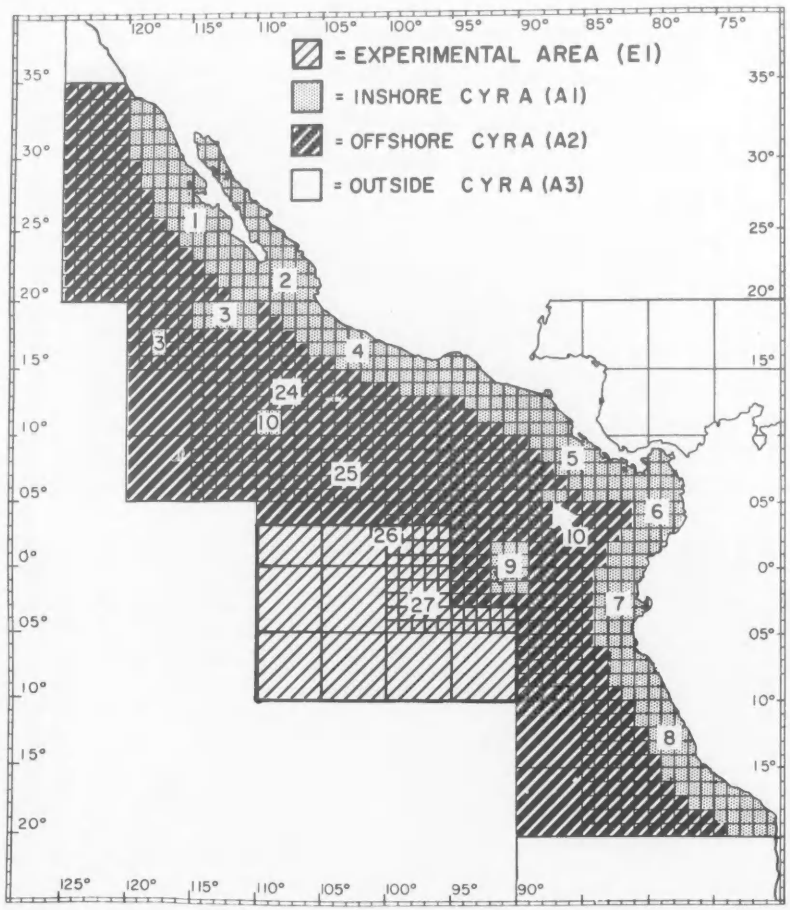


FIGURE 15.—Estimates of coefficient of instantaneous natural mortality on annual basis (M) and modal age of yellowfin tuna by row and column: (A) inshore recruitment, and (B) uniform recruitment.



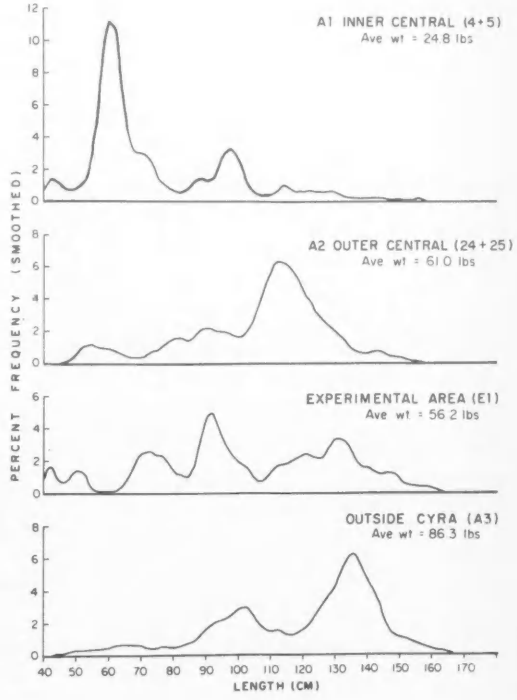

A1 INNER CENTRAL (4+5)
Ave wt = 24.8 lbs
A2 OUTER CENTRAL (24+25)
Ave wt = 61.0 lbs
EXPERIMENTAL AREA (E1)
Ave wt = 56.2 lbs
OUTSIDE CYRA (A3)
Ave wt = 86.3 lbs
PERCENT FREQUENCY (SMOOTHED)
0 2 4 6 8 10 12
40 50 60 70 80 90 100 110 120 130 140 150 160 170
LENGTH (CM)

FIGURE 16.—Taken from the Inter-American Tropical Tuna Commission (1974): (a) the eastern Pacific Ocean showing areas A1, A2, and A3. The numbers within the areas designate subareas used for size composition studies, and (b) length-frequency distribution of yellowfin tuna in the inner area (areas 4 and 5), the outer area (areas 24 and 25) of the central region of the CYRA (Commission Yellowfin Regulatory Area), in the experimental area (E1), and in the area to the west of the CYRA (A3).

1) For the first 5 yr only longliners fished and only in rows 5 to 8.

2) For the next 5 yr, this longline fishery was augmented with surface gear in all cells adjacent to the coast.

3) Next, exploitation by the surface gear was expanded to include all cells for 5 yr.

4) Finally, for the last 5 yr, age specific surface fishing mortality was reduced by 75% for fish <2.5 yr of age because much of the surface catch of yellowfin tuna in offshore areas of the eastern Pacific comes from schools associated with porpoise. Typically, porpoise schools contain few yellowfin tuna <2.5 yr of age (Calkins 1965).

Steps 1, 2, and 3 resemble the sequence of events in the eastern Atlantic fishery for yellowfin tuna. Yellowfin tuna first were exploited in a significant fashion by longliners in a 10° band along the equator, then a nearshore surface fishery became significant, and in recent years some exploitation by surface gear in offshore areas has occurred. To our knowledge, step 4 has not occurred in the Atlantic. Age-specific fishing mortality rates similar to those by surface gears estimated by Lenarz et al. (1974) for the Atlantic yellowfin tuna fishery were used (Table 5). The Ricker yield equation was used to calculate yield for each time-area stratum.

Total yields per recruit were calculated and are shown in Figure 17. Yields per recruit are quite similar for both recruitment models except near shore, where yield per recruit was considerably higher for the inshore recruitment model than for the uniform recruitment model. The difference in yield per recruit between the two models decreases slightly as time increases. Yield per recruit closely approached equilibrium yield within 3 yr after a change was made in the fishery. Total equilibrium yield per recruit with an inshore surface fishery

TABLE 5.—Estimates of age-specific F on an annual basis used as baseline for simulation. See text for modifications of mortality rates during simulation.

Age (yr)	Longline gear	Surface gear	Surface gear with reduced F
1.0	0.00	0.30	0.08
1.5	0.00	0.30	0.08
2.0	0.05	0.22	0.06
2.5	0.15	0.20	0.20
3.0	0.25	0.18	0.18
3.5	0.35	0.30	0.30
4.0	0.45	0.35	0.35
4.5	0.40	0.42	0.42
5.0	0.40	0.27	0.27
5.5	0.20	0.20	0.20
6.0	0.05	0.15	0.15

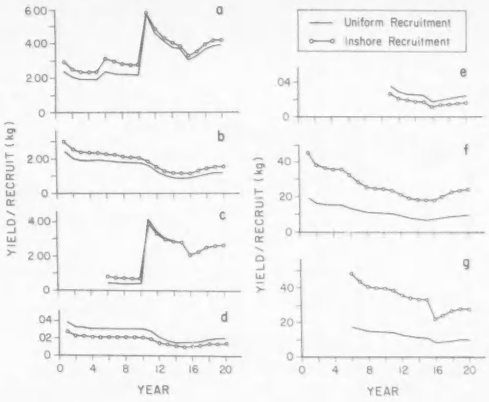


FIGURE 17.—Yield per recruit of hypothetical yellowfin tuna fishery: (a) total, (b) longliners in all areas, (c) surface gear in all areas, (d) longliners in cells 71 and 85, (e) surface gear in cells 71 and 85, (f) longliners in cells 69, 84, and 97, and (g) surface gear in cells 69, 84, and 97.

and longline fishery was about 17% higher than with a longline fishery alone, 54% higher with a uniform surface fishery than with only a longline and inshore surface fishery, and increased by 9% when F for small fish was reduced by 75%. Under the assumption that the catchability coefficient is independent of area, the surface fishery increased its equilibrium yield per recruit about fourfold by increasing its effort about 12-fold when it expanded into offshore waters. The same action decreased yield per recruit to the longliners by about 55%.

We next examined the potential yield per recruit to longliners in rows 5, 6, 7, and 8 by starting a longline fishery with the age-specific F vector multiplied by the scalar 0.3 and then multiplying by 1.3 each year afterward. Yield per recruit appears to approach an asymptote of about 6 kg for inshore recruitment and 5 kg for uniform recruitment (Figure 18). The reduction in catch per recruit per effort by fishing is not significantly affected by choice of recruitment model. Even though catch per recruit per effort at high levels of effort was only about 20% of that at the beginning of exploitation, overfishing in a yield-per-recruit sense did not occur. Average size of fish in the catch was not significantly affected by the recruitment model, and decreased from about 50 to 30 kg with increased fishing effort (Figure 18).

A simulation for an inshore surface fishery indicated an asymptotic production curve with a

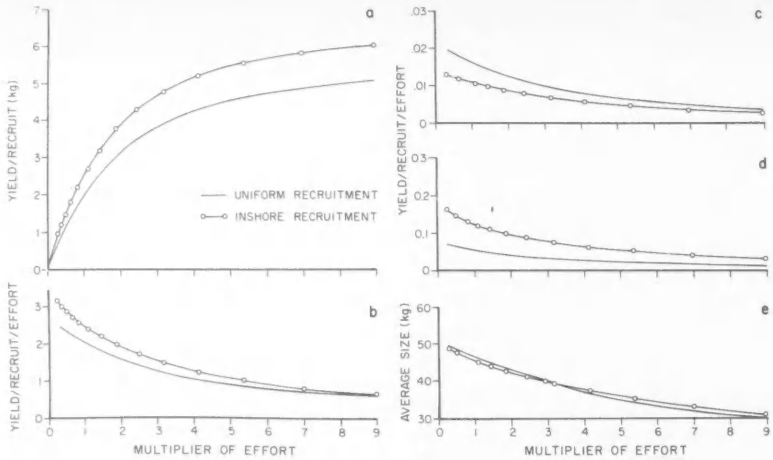


FIGURE 18.—Yield per recruit, yield per recruit per effort, and average size of catch for hypothetical longline fishery: (a) total yield per recruit, (b) total yield per recruit per effort, (c) yield per recruit per effort in cells 71 and 85, (d) yield per recruit per effort in cells 69, 84, and 97, and (e) average size in all squares.

maximum yield per recruit of about 1.4 kg for uniform recruitment and 2.2 kg for inshore recruitment (Figure 19). Catch per recruit per effort was reduced by about 75% under both alternatives. The ratio of maximum yield per recruit for a longline fishery to an inshore surface fishery was about 2.7 for inshore recruitment and 3.4 for uniform recruitment. Average size of fish in the catch was about 2 kg higher for uniform recruitment than for inshore recruitment and decreased from 16 or 18 kg to 8 or 11 kg with increased fishing effort (Figure 19).

Simulation of a uniform surface fishery revealed that choice of recruitment model had an insignificant effect on yield per recruit, catch per recruit per effort, and average size of catch, except that catch per recruit per effort in the nearshore area was relatively high for inshore recruitment (Figure 20). A 75% reduction in F for fish <2.5 yr old had considerable effect on the results. Maximum yield increased from about 5.1 to 6.9 kg when F was reduced. Both yield curves are dome-shaped. Catch per recruit per effort became relatively higher at high levels of effort when F was reduced. As expected, average size was considerably higher for reduced F.

With inshore recruitment, maximum yield per recruit changes from about 2.2 kg for an inshore fishery (Figure 19) to about 5.1 kg for a uniform

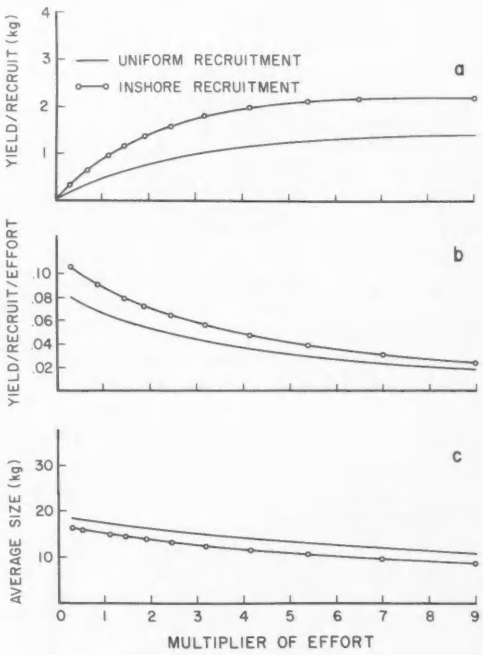


FIGURE 19.—Yield per recruit, yield per recruit per effort, and average size of catch for hypothetical inshore surface fishery: (a) yield per recruit, (b) yield per recruit per effort, and (c) average size of fish in catch.

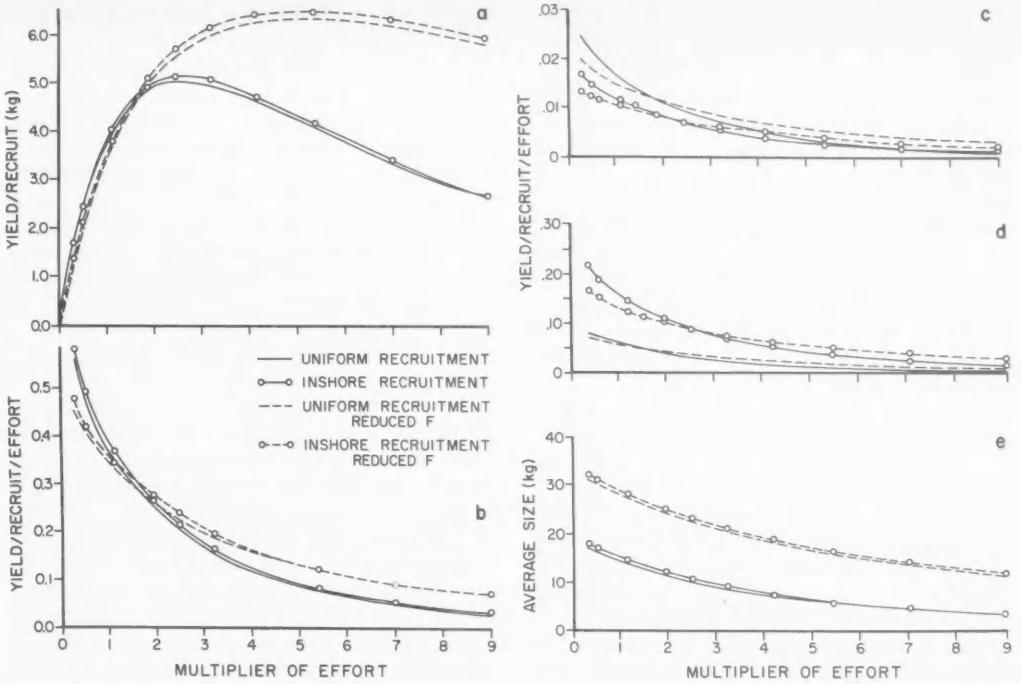


FIGURE 20.—Yield per recruit, yield per recruit per effort, and average size of catch for hypothetical uniform surface fishery: (a) yield per recruit, (b) yield per recruit per effort, (c) yield per recruit per effort in cells 71 and 85, (d) yield per recruit per effort in cells 69, 84, and 97, and (e) average size of fish in catch.

fishery (Figure 20). With uniform recruitment, maximum yield per recruit changes from about 1.4 kg for an inshore fishery to about 5.0 kg for a uniform fishery.

The results of this section indicate that the pattern of recruitment is primarily of interest for examining the potential of a nearshore surface fishery to a surface fishery that exploits the entire area or a longline fishery. The presence of some small yellowfin tuna in length-frequency data for offshore areas from the eastern Pacific fishery (Figure 17) reveals that some recruitment occurs offshore. Recruits apparently are not highly available to surface fishing offshore because most yellowfin tuna are caught in schools associated with porpoise. Such schools normally contain only low percentages of small yellowfin tuna. A well-designed tagging study could provide estimates of the exploitation rate by size for yellowfin tuna in the offshore areas. Until the pattern of recruitment is determined, it will be necessary to continue estimations of relative production to longliners, inshore surface gear, and offshore surface gear in an empirical fashion.

We examined only one reasonable example of an infinite number of possible configurations of the transfer matrix A and time interval. Further use of the model should include a sensitivity analysis of the results to choice of A and number of cycles per year.

SUMMARY AND CONCLUSIONS

This paper examines three aspects of dual fisheries (surface and longline) on yellowfin tuna. Models of yellowfin tuna fisheries are developed to evaluate possible effects of unknown components of the biology and behavior on the fisheries. The results, while not conclusive because of insufficient knowledge, indicate the magnitude of the effects of those factors which were examined.

We present evidence that not all yellowfin tuna are equally available to longline and surface fisheries in the Pacific Ocean. We show that three

models of availability of yellowfin tuna to the two types of gear in the Atlatnic Ocean do not have much effect on decisions concerning minimum size regulations. If fish are equally available to both gear types, yield per recruit is higher to a longline fishery than to a surface fishery, but is higher for the combined gears than to either gear fishing alone.

We also note that there is considerable evidence that large females of all commercially important *Thunnus* are caught in fewer numbers than large males. The effect of this phenomenon on yield per recruit and relative stock fecundity was examined for Atlantic yellowfin tuna. When plotted against fishing effort, yield per recruit is more dome-shaped when the sex ratio is 1:1, as is usually assumed, than when the sex ratio is as observed. Changes in size at recruitment also have a greater effect on yield per recruit when the sex ratio is 1:1 than when the sex ratio is as observed. Competition between longline and surface fishing is more intense when the sex ratio is 1:1 than otherwise. The fishery has a greater effect on stock fecundity if the sex ratio is 1:1 instead of that observed.

Tagging studies of yellowfin tuna in the eastern Pacific indicate that movements are fairly slow compared with more highly migratory species such as albacore and bluefin tuna and have not produced any clear-cut evidence of a definite migration pattern. Size composition of the catch suggests that recruitment to the fishery occurs mainly along the coast of Central America. A simulation model was developed for the eastern Pacific to examine the interrelationships of patterns of movements of fish, patterns of recruitment, and fishing strategy. It was assumed that movements were random and recruitment occurred either along the coast or throughout the eastern Pacific. The results indicate that either pattern of recruitment could allow the increased catch observed in the Pacific as the surface fleet moved offshore. However, the pattern of recruitment does affect the potential yield per recruit of a nearshore surface fishery relative to a surface or longline fishery that exploits the entire area. Both choices of recruitment models resulted in an asymptotic relationship between yield per recruit and effort for a longline fishery over the range of effort examined. Overfishing in a yield per recruit sense did not occur, even though catch per effort decreased by 80%. Approximately the same results were obtained for an inshore surface fishery. However, curves of yield per recruit plotted against effort for a surface fishery that exploits the entire area are dome-shaped.

The study reveals several biological and behavioral parameters which, because of lack of knowledge or information, are rarely considered but do appear to have a significant effect on some aspects of the dynamics of yellowfin tuna fisheries. Tagging and fecundity studies are suggested in order to fill these gaps. Perhaps as important, other aspects of the dynamics of yellowfin tuna fishing appear to be insignificantly affected by the examined parameters.

ACKNOWLEDGMENTS

This study was stimulated by Brian J. Rothschild, who has had a long interest in the interactions between longline and surface fisheries for tunas. The work benefited from discussions with Rothschild and William W. Fox, Jr. of the Southwest Fisheries Center La Jolla Laboratory; William H. Bayliff and Patrick K. Tomlinson of the Inter-American Tropical Tuna Commission, La Jolla, Calif.; Allan Fonteneau of the Centre de Recherches Oceanographiques, Abidjan, Ivory Coast; and Frank Mather III of the Woods Hole Oceanographic Institution. Many of the computer runs were made by Atilio Coan and Kenneth Brenneke of the Southwest Fisheries Center La Jolla Laboratory. We thank William H. Bayliff, Jerry Wetherall of the Southwest Fisheries Center Honolulu Laboratory and John P. Wise, National Marine Fisheries Service, Washington, D.C., for reviewing the paper. We owe considerable thanks to an unnamed referee who made many useful suggestions and to Lorraine Prescott for her patient and excellent typings of several versions of this paper.

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ASPECTS OF BROWN SHRIMP, *PENAEUS AZTECUS*, GROWTH IN THE NORTHERN GULF OF MEXICO

MICHAEL L. PARRACK[1]

ABSTRACT

The growth of brown shrimp, *Penaeus aztecus*, was studied by utilizing forms of growth models compatible with mark-recapture data. The analysis of 5,100 individuals marked and later recaptured in the northern Gulf of Mexico indicates that the von Bertalanffy model is slightly superior to the logistic in reflecting growth in length and the monomolecular model is superior to the Gompertz in expressing growth in weight. Linear functions are apparently inadequate growth models for brown shrimp. Estimated size-age relationships are appreciably different for each sex in that females are much larger than males of the same age. The pattern of growth shown in this analysis for populations in the northern Gulf is different from that reported in the southern Gulf off the Mexican coast and that reported in U.S. Atlantic coastal waters.

The commercial importance of brown shrimp, *Penaeus aztecus* (Ives 1891), has precipitated several studies of the growth rate for individuals of that species. Definition of the growth rate is necessary in order to develop an understanding of the population dynamics of the resource. Growth models have been reported for wild populations in the northwest Atlantic off North Carolina (McCoy 1972) and in the southern Gulf of Mexico off Tampico, Mexico (Chávez 1973). Several workers have described the growth rate of small brown shrimp in the northern gulf (George 1962; St. Amant et al. 1963, 1966; Loesch 1965; Ringo 1965; Jacob 1971; Wengert 1972; Gaidry and White 1973; Rose et al. 1975; Welker et al. 1975; Knudsen et al. 1977). The growth rate of larger brown shrimp, however, has not been documented for populations in the northern gulf.

Generally, growth equations define the relation between the size and age of individual animals. Three such equations descriptive of growth are the logistic (Pearl and Reed 1920), von Bertalanffy (Bertalanffy 1938), and Gompertz (Gompertz 1825; Silliman 1967) functions. The logistic and von Bertalanffy models are employed to reflect growth in length whereas the Gompertz is usually used to model growth in weight. The von Bertalanffy function may be directly fit to weight data to model growth in weight. If it is so used, it is then correctly referred to as the monomolecular growth model (Medawar 1945; Fabens 1965). This study appraised the abilities of these functions to model brown shrimp growth. Additionally the linear relation between size and age was also considered.

The absolute age of shrimp cannot be determined directly by counting annuli on hard parts. Shrimp molt many times during their life cycle; all hard parts are lost, then reformed with each molt. Therefore, age-size data of individuals cannot be obtained for growth modeling; another technique must be employed. Although the age of brown shrimp at mean size has been discerned from large volume size-frequency samples (Chávez 1973), age was not directly observable and therefore was inferred. Mark-recapture data affords a direct measure of the changes in size per change in time. Forms of the growth functions were employed to utilize mark-recapture data so that error resulting from incorrect age determination was avoided.

METHODS

Brown shrimp spawn in offshore Gulf of Mexico waters (14-100 m deep) throughout the year (Cook and Lindner 1970). Eggs hatch within 14-18 h (Cook and Murphy 1966) and larvae undergo metamorphosis within 12-15 days (Cook and Lindner 1970). Shrimp then migrate into estuaries to undergo their juvenile period. Large juvenile shrimp, usually 75-90 mm total length, migrate to offshore waters as they become sexually mature, thus completing the life cycle. Ap-

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proximately 80% of the recaptured individuals utilized in this analysis were large juveniles when marked. These shrimp were marked and released in estuarine waters before migrating to offshore waters (Table 1). The remaining 20% were large adults marked and released in offshore gulf waters along the Texas coast. These marking experiments were carried out during 1967, 1968, and 1969. A full explanation of the data is given by Clark et al. (1974). These data include total length (i.e., the distance from the anterior end of the rostrum to the posterior end of the telson) when released and when recaptured, the dates of release and recapture, and the sex of each individual. Data entries with the same release and recapture dates do not reflect growth and therefore were not used to estimate growth rates.

In order to analyze growth in weight, release and recapture length were converted to weights according to weight-length relations. These relations were estimated from data collected from the commercial landings at Galveston, Tex., during June, September, and December of 1965 and March of 1966 (Fontaine and Neal 1971). Parameters of the model weight $= a\,(\text{length})^b$ were estimated for males and for females separately by minimizing the expression $\sum_{n}^{n} (W - W_o)^2$ where W is weight defined by the model, W_o is observed weight, and n is the number of observations. The Marquardt algorithm (Marquardt 1963) was employed to find the minimum. Plots of the estimated relations through the scatter of the observations were observed to discern male/female differences and the predictive usefulness of the models.

Since mark-recapture data were employed, growth functions of interest were expressed in terms of the change in age rather than absolute age (see Appendix for derivation of equations). Each recaptured individual was of some unknown age on the date marked and on the date recaptured so that the change in age is equivalent to the time at large. Expressed in these terms the logistic function changes from

$$S_a = S_\infty/(1 + be^{-ka}) \qquad (1a)$$

to

$$S_r = S_\infty/(1 + [(e^{-k(\triangle a)})\ (S_\infty - S_m)/S_m]) \qquad (1b)$$

by substitution and rearrangement of terms. Likewise, the von Bertalanffy equation

$$S_a = S_\infty(1 - be^{-ka}) \qquad (2a)$$

is expressed as

$$S_r = S_\infty - (S_\infty - S_m)e^{-k(\triangle a)}. \qquad (2b)$$

The Gompertz function

$$S_a = S_i \exp[G(1 - \exp[-g(a - a_i)])] \qquad (3a)$$

becomes

$$S_r = S_i[\exp G][S_m/(S_i \exp G)]^{\exp[-g(\triangle a)]}. \qquad (3b)$$

A linear function of size upon age

$$S_a = b + ka \qquad (4a)$$

is written

$$S_r = S_m + k\,(\triangle a)\,. \qquad (4b)$$

Definitions of symbols employed above are:

S_a = size at age a,
S_r = size at recapture,
S_m = size when marked,
S_i = size of the smallest animal in the data,
a_i = age of the smallest animal in the data,

TABLE 1.—Brown shrimp mark-recapture experiments, northern Gulf of Mexico.

Release area	Release date	Length range (mm) of released shrimp	Length range (mm) of recovered shrimp	Number recovered
Galveston Estuary	May 1967	66-175	71-124	13
50 mi east of Galveston, Tex.	June 1967	83-147	86-178	301
60 mi southeast of Freeport, Tex.	Sept. 1967	122-181	124-196	40
Biloxi Bay, Miss.	May 1968	90-122	90-181	4,218
40 mi southeast of Freeport, Tex.	Feb.-Mar. 1969	109-168	136-185	69
Galveston Estuary	June-July 1969	90-128	91-182	257
50 mi southeast of Freeport, Tex.	Nov. 1969	145-203	141-213	593

S_∞ = an equation parameter, the asymptotic size,
b = an equation constant related to the size at birth,
$\Delta a = a_r - a_m$ = time at large,
a_r = age of an individual on the date recaptured,
a_m = age on the date marked and released,

and G, g, and k are equation parameters.

Equation parameters S_∞, k, G, and g were estimated by utilizing the Marquardt algorithm to minimize the residual sum of squares:

$$\sum^{n} (S_r' - S_r)^2$$

where n = the number of individuals marked and recaptured,
S_r' = the observed size at recapture, and
S_r = the size at recapture as estimated by the growth equation.

The remaining equation constants, b in Equations (1a) and (2a) and a_i in Equation (3a), are respectively computed:

$$b = (S_\infty / S_b) - 1 \qquad (5a)$$

$$b = (S_\infty - S_b)/S \qquad (5b)$$

$$a_i = \ln\left[1 - \frac{\ln(S_b/S_i)}{G}\right]g \qquad (5c)$$

where S_b is the size at birth and other symbols are as before. The parameter b in Equation (4a) is simply the size at birth.

Studies of the early development of brown shrimp indicate that newly hatched larvae are 0.35 mm total length (Cook and Murphy 1971). Estimates of the equation constant b in the logistic and von Bertalanffy models were based on that length at birth.

Shrimp eggs are 0.26 mm in diameter (Cook and Murphy 1971) and about the density of water (Cook and Lindner 1970) so that the weight at hatching is about 0.000009 g. Brown shrimp undergo metamorphosis 11 to 15 days after hatching (Cook and Lindner 1970) and are 0.0008 g at that time (Wheeler 1969). The weight at birth was calculated as the midpoint between that weight and the egg weight. Calculations of b and a_i in the various models were based on that weight at birth.

RESULTS

Growth in Length

In anticipation that differences in growth between sexes may exist, equations were fit for males and females separately. Estimated equation parameters (Table 2) are quite different between sexes. The fitted models indicate that females are much larger than males of the same age. The estimates of the growth coefficient k do not differ greatly between sexes for both the logistic and the von Bertalanffy models; the 90% probability support plane confidence intervals (Conway et al. 1970) extensively overlap for both models. The estimates of asymptotic length are, however, greatly different and such confidence intervals on those estimates are very disjoint. Pooling all data together to estimate overall growth functions for both sexes combined was therefore judged unrealistic.

The relative abilities of the von Bertalanffy, logistic, and linear models to correctly reflect growth was judged by comparing residual sums of squares (Table 3). The von Bertalanffy function produced the smallest residual and the linear model the largest. The residual sum of squares for the linear model was well over three times that of the von Bertalanffy and logistic models for both males and females. The difference between the two nonlinear models was much smaller; the residual of the logistic was but 8% larger than that of

TABLE 2.—Growth models for brown shrimp. Lengths (L) in millimeters, weights (W) in grams, and ages (a) in months.

Model	Males	Females
Logistic	$L = 162.8/(1 + 464.1429e^{-0.5664a})$	$L = 187.5/(1 + 534.7143e^{-0.6116a})$
von Bertalanffy	$L = 168.7(1 - 0.9979e^{-0.3357a})$	$L = 193.6(1 - 0.9982e^{-0.3363a})$
Linear	$L = 0.35 + 4.2181a$	$L = 0.35 + 7.8209a$
Gompertz	$W = 5.07(\exp[1.9996(1 - \exp[-0.3735(a - 4.6688)])])$	$W = 3.55(\exp[2.8359(2 - \exp[-0.4410(a - 3.2549)])])$
Monomolecular	$W = 43.51(1 - 0.9999e^{-0.1546a})$	$W = 74.32(1 - 0.9999e^{-0.1416a})$
Linear	$W = 0.0004045 + 1.8018a$	$W = 0.0004054 + 3.901a$

the von Bertalanffy in the case of males and 5% larger for females.

TABLE 3.—Residual sums of squares for six brown shrimp growth models.

Model	Males	Females
Length:		
Von Bertalanffy	44,161.65	155,797.40
Logistic	47,661.96	163,278.00
Linear	162,661.15	599,677.13
Weight:		
Monomolecular	5,548.57	33,930.69
Gompertz	7,027.72	38,751.26
Linear	12,335.42	67,526.07
Number of observations	1,536	3,588

The difference in growth between sexes and the ability of the von Bertalanffy model to fit the observations is visible from plots of the observed lengths about the growth models. Data points were plotted by first calculating the age at release from the fitted model, adding time at large to compute the age at recapture, then plotting that age and the recapture size. The plots (Figure 1A, B) show that sex specific growth does exist and that the differences are of significant magnitude. Further, the von Bertalanffy model does visibly fit the observed data. Although the observed data do

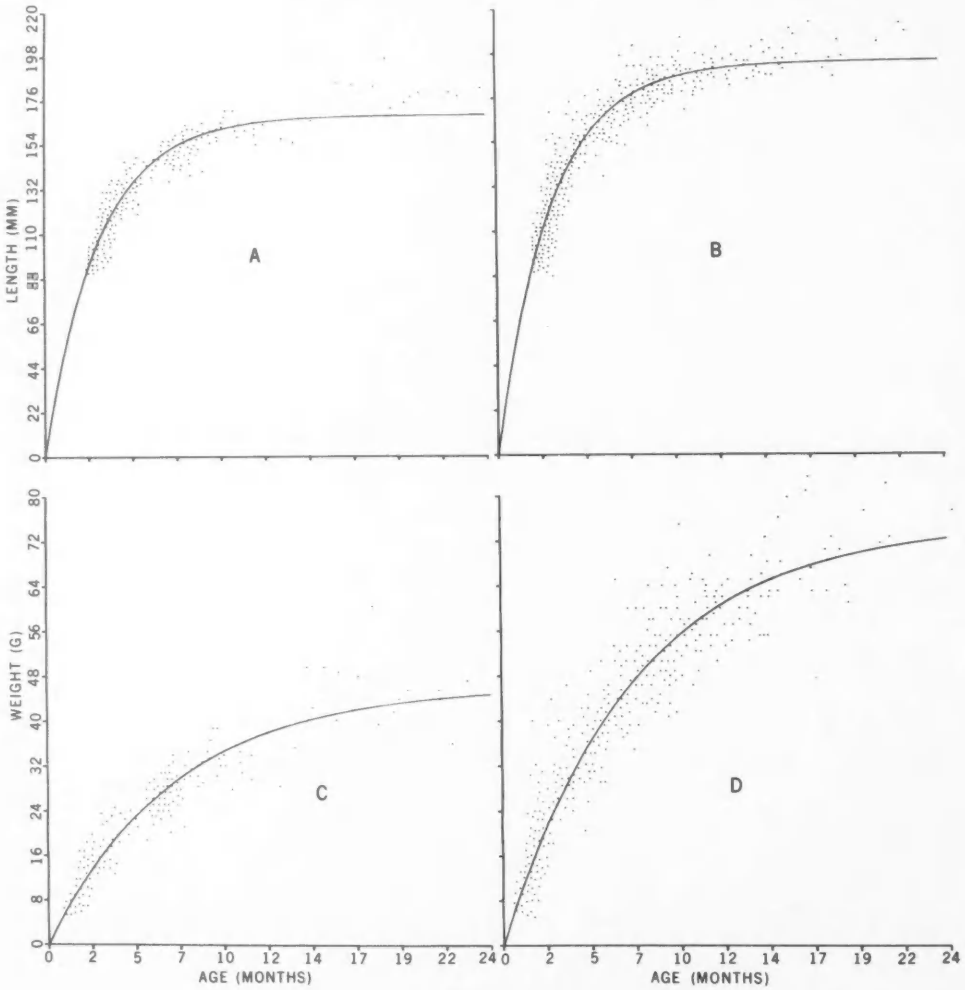

FIGURE 1.—Brown shrimp growth models. A) von Bertalanffy growth model, males; B) von Bertalanffy growth model, females; C) monomolecular model, males; D) monomolecular model, females.

not in general fall close to the modeled line, the scatter is not severe.

Growth in Weight

The Marquardt algorithm (Marquardt 1963) was employed to estimate parameters of weight-length relations used to transform individual release and recapture lengths into weights so that growth in weight could be modeled. Plots of the estimated relations (Figure 2) indicate them to be sex specific. Support plane confidence intervals (Conway et al. 1970) on equation parameters (90% probability) for males did not overlap those for females further indicating that the functions differ between sexes. In addition the data were logged to linearize the relation and covariance analysis techniques applied to test for differences between sexes. The probability that the linearized functions are the same is small ($P_r < 0.001$) further indicating the sex specificity of these relations. Further inspection of the plots shows the scatter of observations to be restricted and that the models effectively fit. These sex specific models were therefore employed to transform the data.

The magnitude of residual sums of squares (Table 3) indicates the monomolecular model is the best predictor of weight at age and the linear model the poorest. The residual term for the linear fit is about twice as large as that for the monomolecular model and about 1.8 times that of the Gompertz for both sexes. The reduction in residuals of the monomolecular model as compared with the Gompertz was much smaller, 25% in the case of males and 14% in the case of females.

As in the case of growth in length, estimated growth parameters indicate that growth in weight is sex dependent. Both the Gompertz and the monomolecular model estimate females to be much larger than males of the same age. Asymptotic weight (monomolecular model) is estimated to be 75 g for females and 46 g for males; support plane confidence intervals (90% probability) on these estimates do not overlap. Estimates of the parameter k in the monomolecular model appear to be about the same for both sexes and in fact the support plane confidence interval for males completely includes that interval for females.

The differences in growth between sexes and the degree of fit of the monomolecular model is shown in Figure 1. Although appreciable scatter is ap-

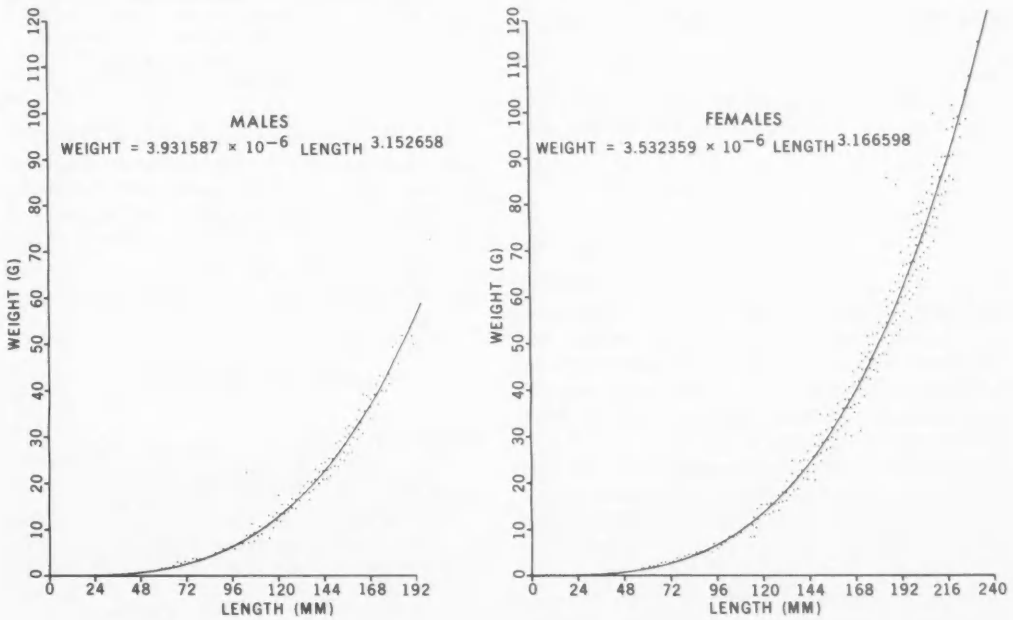

FIGURE 2.—Weight-length relationships for brown shrimp.

parent, systematic departure of the observed points from the model is not evident so that the model does reflect the data.

CONCLUSIONS

The relative abilities of prediction of the different models can be judged by comparison of their residual sum of squares. The comparison strongly suggests that the linear function was by far the poorest model of brown shrimp growth both in length and weight. Although the size-age relation does appear linear for small young individuals, the rate of increase in size decreases with age, a phenomenon documented for many organisms both terrestrial and aquatic. A nonlinear function is therefore required to model brown shrimp growth throughout their entire life span.

The residual sum of squares for the von Bertalanffy equation was smaller than the logistic equation when modeling weight; however, these differences were not large. It is therefore not completely evident that the von Bertalanffy equation is vastly superior to the logistic and Gompertz in the modeling of brown shrimp growth. The von Bertalanffy equation did, however, constantly fit these data best for both sexes in the modeling of both length and weight. This study does therefore show the von Bertalanffy model to be slightly superior to the logistic and the monomolecular model superior to the Gompertz for both sexes.

The difference in the size-age function between sexes was found to be large. This phenomenon was previously reported for brown shrimp in the southern Gulf of Mexico (Chávez 1973) and northwest Atlantic (McCoy 1972) and for many other marine organisms. This study indicates that male brown shrimp apparently grow to approximately only three-fifths the weight and five-sixths the length of females; however, the coefficients of growth, as indexed by k in the monomolecular and von Bertalanffy models, are roughly equivalent. It is interesting to note that the rate of increase in size tends to fall off at an earlier age for males than for females (see Figure 1). Since, in general, a decrease in that rate roughly conforms to the age of maturity and sexual activity, it is not unreasonable to assume that males mature at a younger age than do females.

Comparison of growth functions derived herein with those generated by other workers indicate that brown shrimp growth in the northern Gulf of Mexico is very different than that in the southern gulf and in U.S. Atlantic coastal waters. Growth functions derived from populations off Mexico (Chávez 1973) demonstrated a faster and prolonged growth compared with growth observed in this study. That trend was consistent for both males and females. Studies off North Carolina (McCoy 1972) showed growth in Atlantic waters to be very rapid although a smaller asymptotic size was realized. As before, that trend was the same for both sexes. The kinds of data used and the methods employed to fit the growth models differed in all three studies; therefore, some disagreement in results may be expected. The magnitude of the differences observed, however, indicated truly different rates of growth may well exist in the three geographical locations. The growth of wild populations of white shrimp, *Penaeus setiferus*, a similar species, is correlated with water temperature (Gaidry and White 1973) in the shallow estuarine and nearshore areas they inhabit throughout their entire life span. Since the temperature of seasonally homothermic deep offshore waters where brown shrimp spend their adult life may be assumed to increase with decreasing latitude, the differences in growth between northwest Atlantic, northern gulf, and southern gulf brown shrimp populations are likely positively correlated with gross water temperature.

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APPENDIX

The linear, logistic, and Gompertz functions were expressed in terms of size at release age, size at recapture age, and change in age (time at large) following the rationale presented by Fabens (1965) for the von Bertalanffy function (as follows).

Each individual was of some unknown age (a_m) upon the date marked (t_m) and released. Upon the recapture date (t_r) the individual was of an unknown older age (a_r) so that the difference between the release and recapture date (Δt) is equivalent to the increase in age (Δa) of that individual:

$$\triangle a = \triangle t = t_r - t_m = a_r - a_m . \tag{A1}$$

That equality can be substituted into the von Bertalanffy function when expressed in terms of the size at recapture (S_r) and the age at recapture. Therefore the von Bertalanffy equation

$$S_r = S_\infty [1 - b \exp(-ka_r)] \tag{A2}$$

becomes $S_r = S_\infty (1 - b \exp(-ka_m) \exp[-k(\triangle a)])$. (A3)

The equation, when expressed in terms of the size when marked (S_m) with rearrangement, is:

$$b \exp(-ka_m) = 1 - (S_m / S_\infty). \tag{A4}$$

That expression is substituted into Equation (A3) to yield the required function:

$$S_r = S_\infty - (S_\infty - S_m) e^{-k(\triangle a)}. \tag{A5}$$

That form can then be employed to estimate the equation parameters k and S from mark-recapture data. The final parameter (b) can be calculated directly by first rearranging terms of the original function:

$$S_a = S_\infty (1 - be^{-ka}) \tag{A6}$$

so that $b = [1 - (S_a / S_\infty)] / e^{-ka}$ (A7)

where S_a is the size at age a. If the size at birth, i.e., at age 0, is known, then:

$$b = 1 - (S_b / S_\infty) \tag{A8}$$

where S_x is estimated from Equation (A5) and the size at birth (S_b) is derived from life history studies.

That same rationale was applied to the logistic function. The size of a recaptured individual is expressed:

$$S_r = S_\infty / [1 + b \exp(-ka_r)] . \tag{A9}$$

Since $a_r = a + a_m$ substitution gives:

$$S_r = S_\infty / (1 + b \exp[-k(\triangle a)] b \exp(-ka_m)] . \tag{A10}$$

Expressing the logistic equation in terms of the size marked and rearrangement of terms gives:

$$b \exp(-ka_m) + [(S_\infty - S_m) / S_m] . \tag{A11}$$

Substitution yields:

$$S_r = S_\infty / [1 + ((e^{-k(\triangle a)}) (S_\infty - S_m) / S_m)] . \quad \text{(A12)}$$

Since S_r, S_m, and Δa were all directly observable from mark-recapture data, the logistic equation parameters S_∞ and k may be estimated from the data set. The remaining equation constant was calculated by rearrangement of terms:

$$b = ((S_\infty / S_a) - 1) / e^{-k(a)} . \quad \text{(A13)}$$

From life history studies the size at birth, S_b, was determined. Since at birth age is zero ($a = 0$) the expression can be written:

$$b = (S_\infty / S_b) - 1. \quad \text{(A14)}$$

The Gompertz function was likewise expressed in terms of the mark-recapture data. From Equation (3a), the size at the time of marking is:

$$S_r = S_i \exp[G(1 - \exp[-g(a_r - a_i)])] \quad \text{(A15)}$$

and by substitution becomes

$$S_r = S_i \exp[G - G(\exp[-g(a_m - a_i)]) (\exp[-g(\triangle a)])] . \quad \text{(A16)}$$

Writing in terms of the size at recapture and rearrangement of terms gives:

$$\exp(-G \exp[-g(a_m - a_i)]) = S_m / (S_i \exp G). \quad \text{(A17)}$$

Substitution yields the expression required to estimate the constants G and g from the mark-recapture data:

$$S_r = [S_i \exp(G)][S_m / (S_i \exp(G))]^{\exp[-g(\triangle a)]} \quad \text{(A18)}$$

where S_i was the smallest size observed in those data. The remaining equation constant, a_i, was then calculated by writing Equation (3a) in terms of the size at birth:

$$S_b = S_i \exp[G(1 - \exp[-g(a - a_i)])] . \quad \text{(A19)}$$

Since at birth age is zero ($a = 0$) the expression can be written as:

$$a_i = \ln(1 - [\ln(S_b / S_i) / G] / g) \quad \text{(A20)}$$

where S_b, the size at birth, was determined from natural history studies. The linear function:

$$S_a = b + ka \quad \text{(A21)}$$

requires a much simpler derivation. Expressed in terms of the size at recapture:

$$S_r = b + ka_r . \quad \text{(A22)}$$

Substitution gives:

$$S_r = b + k(\triangle a + a_m) . \quad \text{(A23)}$$

The function expressed in terms of the size at release

$$S_m = b + ka_m \tag{A24}$$

can be rearranged to

$$a_m = (S_m - b)/k \tag{A25}$$

which can be substituted into Equation (A23) to give

$$S_r = k \triangle a + S_m \, . \tag{A26}$$

The remaining parameter b is simply the ordinate intercept or the size at birth.

THERMAL BEHAVIORAL RESPONSES OF SELECTED CALIFORNIA LITTORAL FISHES

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ABSTRACT

Two horizontal temperature gradients were used to measure behavioral responses to temperature of various life stages of 16 species of temperate marine fishes from southern California, and we offer guidelines for standardization of collection, acclimation, preexperimental holding, and testing conditions. We classified behavioral responses to thermal gradients using eight experimental parameters: initial, mean, modal, and final selected temperatures; range of selected temperatures; skewness; kurtosis; and the degree of dispersion between individuals. We found four behavioral responses to changes in temperatures with time: 1) immediate—no general shift in selected temperature with time, 2) fast—a shift in selected temperature over the first 2 h of the experiment only, 3) slow—a shift in selected temperature over more than 2 h in the experiments, and 4) positioned—a wide range of selected temperatures and a tendency to remain in a given position in the gradient until conditions become extreme. Effects of preexperimental acclimation temperatures on thermal selection did not last longer than 4h. One day of food deprivation resulted in lower selected temperatures and changed the precision of selection and aggregating tendencies, although the direction of the change varied between species.

Over the last several decades, the behavior of fishes with respect to thermal gradients has been investigated by many workers (see review by Coutant 1977). Most studies in the literature, however, have dealt with freshwater or estuarine species that occur in large part in eastern North America. Little work has been carried out on temperate marine species, which, except for intertidal inhabitants, generally experience smaller natural diurnal and seasonal temperature fluctuations.

Our two horizontal gradients and experimental procedures were built on many of what appear to be the best attributes of previous studies. Variation in reported experimental techniques makes comparisons between studies difficult. We suggest guidelines for method standardization in this paper.

Horizontal gradients were chosen because they allowed experimentation with groups, permitted demersal fish to be in contact with a bottom and pelagic species to swim freely. This type of gradient also allowed us to combine some of the best attributes of spatial gradients (e.g., Norris 1963) and temporal ones (e.g., Beitinger 1976). Further, our study, in conjunction with a field survey, was designed to assess the effects of temperature on the distribution, behavior, and physiology of fishes found in King Harbor, Redondo Beach, Calif. This harbor, which receives the thermal discharge from an electricity generating station, as well as cold, upwelled water from the adjacent Redondo Submarine Canyon, contains a highly diversified thermal environment (Stephens 1972), including many horizontal gradients.

Our intent is to introduce a comprehensive approach to thermal response testing, including equipment design, preexperimental and experimental methodology and protocol, and to show representative examples of behavioral responses. We have examined to date the behavior of various life stages from larvae to adults of 16 fish species from 10 families. Comparative studies of laboratory and field results are in preparation.

EXPERIMENTAL CRITERIA

A wide range of experimental methodology exists in the literature (see review by McCauley 1977). McCauley and Tait (1970) stated, "Comparison of preference temperatures in the literature is

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questionable, because of differences in experimental techniques." Preexperimental feeding regimes differ significantly between studies. Cherry et al. (1975) discontinued feeding 2.5 to 3 days before testing; in contrast, Reynolds and Thomson (1974) fed fish approximately 2 h prior to experimentation. The time that the fish were allowed to adjust to the experimental chamber before initiation of data collection was also variable. Tat'yankin (1972) used a habituation period of only 0.5 h, while McCauley and Read (1973) used a period of 2 days. Length of time between observations was not consistent between studies. Ferguson (1958) observed fish hourly, but Norris (1963) recorded fish position every 6 s. Although most investigations used organisms once, Javaid and Anderson (1967) reused fish between successive experiments. Some of the differences in experimental techniques may have been due to species-specific problems; however, in many studies the primary concern was simply to provide a thermal gradient, to place test organisms in it, and to measure their response. Often, little attention was paid to factors relevant to the well-being of the fish (e.g., shock from capture and handling, nutritive condition) and to simulating natural intensities and quality of light.

General procedural recommendations have been made by Richards et al. (1977). Our methods build on techniques from past studies, including their best attributes. Some of the differences in experimental techniques are subtle, but important, especially since this investigation concerns marine species, on which little work has been done. The methods, procedures, and physical conditions of collection, handling, and experimentation in this study were chosen to minimize trauma to test organisms. The following methods and rationales that we employed are provided as suggestions toward standardization:

1) Our preferred methods of obtaining test organisms involved collecting by means of lift nets or traps or to rear them from eggs. These minimized damage to the fishes.
2) Fish feeding was established in the laboratory. We tested only fish that fed, as this indicated that they were most likely not in shock from collection.
3) We brought fish to desired acclimation temperatures, from that at which they were collected, at a rate of 1°C/day. The test specimens were held for at least 2 wk prior to testing. The length of the holding period was particularly important to assure acclimation to cold temperatures (Brett 1970).
4) We did not use anaesthetics in collections or preexperimental handling; Goddard et al. (1974) have shown that MS-222[4] can influence thermal behavioral responses for several weeks after treatment.
5) We fed the fish ad libitum just prior to their placement in the gradient. This standardized the feeding history, which has been shown to alter temperature selection (Ivlev and Leizerovich 1960; Javaid and Anderson 1967).
6) We placed the fish in the experimental chamber, adjusted to their acclimation temperature, on the evening preceding testing. This allowed adjustment to the new surroundings prior to experimentation. No fish were reused.
7) Testing fish in groups allowed us to assess the effects of temperature on populations, but we could only use this methodology to study gregarious species that did not display agonistic behavior.
8) We established the temperature gradient about the fish. Introduction of test organisms to an established gradient, even at the location of their acclimation temperature, can result in the fish darting to another part of the tank and experiencing a temperature shock.
9) We shifted isotherms during an experiment, and the hot and cold ends were reversed between experiments. This allowed us to attempt to partition any tendencies of the fish to select a particular compartment independent of temperature.
10) We shielded the test chamber from external light and observed the fish from above downward-directed experimental lights to insure that the fish would not respond to presence of the experimenter.
11) We used low levels of lighting, during the experiment, based on minimum intensities for schooling and larval feeding (Blaxter 1970). These levels of illumination did not appear to disturb the fish as was sometimes the case with brighter light. Additionally, Sullivan and Fisher (1954) reported increased precision of temperature selection at low light

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA, or by Occidental College.

intensities. We employed natural day lengths during preexperimental holding as well as during testing.

DESIGN OF GRADIENTS

We built two horizontal gradients: one for juveniles and adults and another, smaller one, for larvae and placed them in a sound-insulated and lightproof room. A differential of at least 10°C between the hot and cold ends of the gradient was established prior to collection of data used for behavioral analyses. We adjusted the size and position of the temperature gradient to keep the experimental fishes from the extreme end compartments; differentials of up to 25°C were employed for species with wide preferred temperature ranges.

Gradient for Juvenile and Adult Fishes

We divided this gradient (360 cm long × 60 cm wide × 60 cm deep, Figure 1) along its longitudinal axis to produce two experimental chambers (15 and 44 cm wide). The size of the test organisms determined which side of the gradient was used. Heating and cooling were controlled, primarily at the ends of the gradient. A rheostat connected to an immersion heater allowed us to minimize the frequency of the heater turning on and off, reducing fluctuations in heat production. A stainless steel (type 316) coil heat exchanger with cold freshwater coolant (1°C) chilled the seawater in the gradient. Two additional heat exchangers constructed of polyvinyl chloride and run along the bottom from the ends to the center of the experimental chamber served to produce a more even temperature gradient.

Formation of thermal currents can limit the temperature range and controllability of a horizontal gradient. Twelve pairs of surface and bottom baffles impeded thermal currents and divided the gradient into 11 experimental compartments.

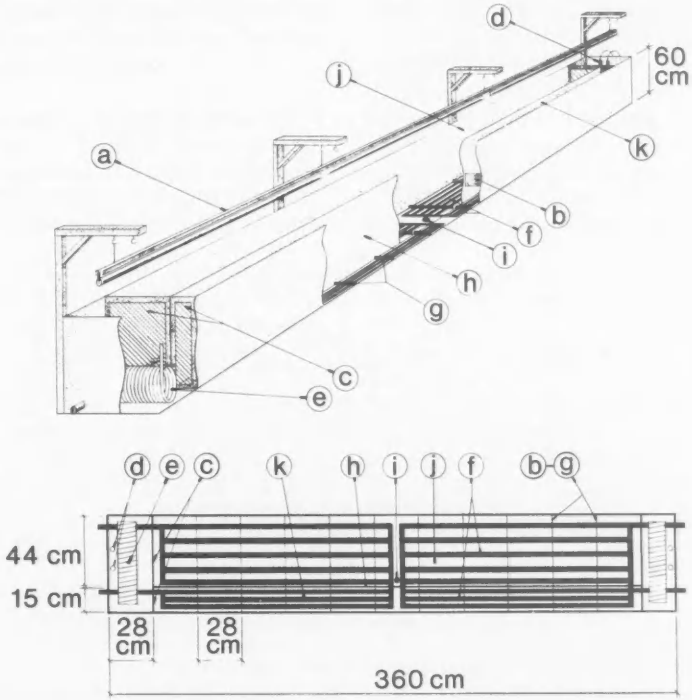

FIGURE 1.—Large experimental chamber for temperature selection measurement in fishes: a) daylight-simulating fluorescent light, b) surface baffle, c) screens separating experimental chambers (j and k) from the end heating and cooling compartments, d) 500-W heaters, e) stainless steel heat exchangers, f) polyvinyl chloride heat exchanger, g) bottom baffles, h) wall separating the large and small experimental chambers, i) drain, j) large experimental chamber, k) small experimental chamber.

The baffles could be lowered or raised with the water level so that they entered the water to a depth of 2 cm. Gentle aeration, from the bottom of each compartment, further eliminated vertical stratification. This also aided removal of any supersaturated gases that Gift (1977) reported to be potential problems in thermal gradients. A nylon screen prevented the test organisms from entering the area where the heating and cooling took place and also provided a flat surface over the bottom baffles. We subdivided the experimental gradient that consisted of 11 compartments each containing a centrally located thermistor probe into 21 visual units that were not visible to the test organisms, by forming an additional compartment centered midway between two thermistors. The mean temperature of two adjacent probes was used for these additional compartments. Daylight-simulating fluorescent fixtures (Duro-test Vitalities), with the use of diffusers, provided a light intensity of 60-70 fc at the water surface.

Gradient for Larval Fishes

The temperature gradient for larval fishes (Figure 2) operated on a counter-current principle. Alternation of hot and cold water entering the experimental chamber between replicate runs eliminated any potential rheotactic interference. The inner experimental trough (1.75 m long × 5 cm diameter; 0.8 mm wall thickness) contained two nylon screens 1.5 m apart that defined the experimental chamber. Seawater velocities of 0.1 to 0.9 mm/s were selected based on known larval swimming speeds (Blaxter 1969; Rosenthal and Hempel 1970; Hunter 1972), because velocities in this range would not present the larvae with any significant difficulty in maintaining a chosen position. Wilson (1974) successfully employed velocities of up to 10.8 mm/s with pelagic marine fish larvae in studying behavioral responses of pollutants.

Hunter and Thomas (1974) showed that larval anchovies aggregated at patches of food (*Gymnodinium splendens*). All entering seawater was filtered to 5 μm to rule out possible position selection by larvae based on presence of prey organisms. Eleven evenly spaced thermistor probes coupled to a telethermometer were used to monitor temperature. We subdivided the experimental chamber into 21 visual compartments and enclosed the trough in a lightproof box. A daylight-simulating fluorescent lamp, with the use of a diffuser, produced 10-15 fc at the water surface.

DEFINITIONS

The term "preferred temperature" has been used in various contexts in the literature (e.g., Brett 1952; Javaid and Anderson 1967; McCauley and Tait 1970; Tat'yankin 1972; McCauley and Read 1973). Much of the variation in the use of this

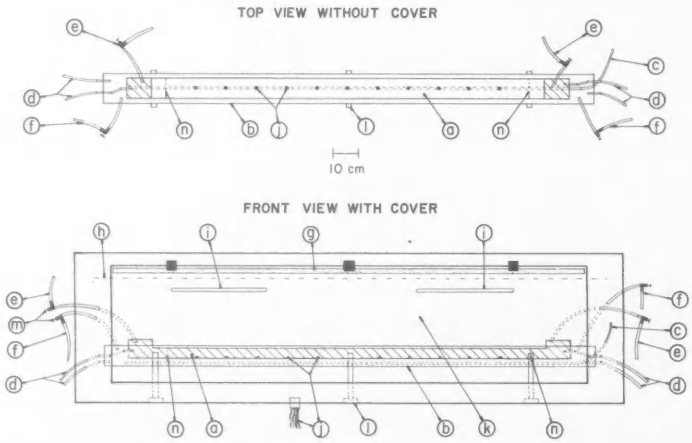

FIGURE 2.—Small experimental chamber for temperature selection measurements in larval fishes: a) experimental chamber, b) water jacket, c) air line, d) drains, e) seawater input line, f) freshwater input line, g) daylight-simulating fluorescent light, h) light diffuser, i) viewing slits, j) thermistor probes, k) door on lightproof cabinet, l) supports for water jacket, m) water flow control valves, n) nylon screen on ends of experimental chamber.

term can be attributed to different species exhibiting various behavioral patterns in a gradient tank, just as they do in their natural habitats. This makes it impossible to use only one procedure to determine the preferred range for all species under all conditions. We determined the preferred range and final perferendum by evaluating, on a case-by-case basis, the behavioral responses of a species subjected to known conditions such as acclimation temperature, feeding patterns, and captivity environment.

Experiments with larvae lasted 5-6 h, but juveniles and adults were tested for approximately 7-8 h. An "experiment," in this study, consisted of a set of individual runs, with each "run" being the observation of the position and water temperature selected by each fish in the gradient at a fixed point in time. We employed constant time intervals between runs for any experiment: 5 min for larvae and 15 min for juveniles and adults. Run selected temperatures were the primary data source, and we calculated their mean, mode, and variance prior to combining them with data from other runs to determine the preferred temperature.

DATA ANALYSES

Reynolds (1977) reported that skewness of temperature preference frequency distributions required a complete description of the distribution. We examined the following parameters to delineate thermal behavioral responses, the initial, mean, modal, and final selected temperatures, standard deviation about the mean, coefficients of skewness and kurtosis, and coefficient of dispersion. The first four parameters defined the preferred temperature range. The standard deviation about the mean selected temperature quantified movement through a range of temperatures and gave a measure of the degree of eury- or stenothermal preference. We used coefficients of skewness and kurtosis (Sokal and Rohlf 1969) in testing for normality and then to help define the shape of the temperature-specific fish frequency of occurrence distribution and to refine interpretation of behavioral types. The coefficient of dispersion quantified the tendency of a species to aggregate or school and gave the percentage of use of the experimental chamber by all fish within one standard deviation of the run selected temperature.

The frequency of occurrence of all experimental temperatures was not uniform due to the shifting of the gradient as well as having a variable number of degree intervals per run and generally fewer than the 21 compartments. This caused a bias in the number of fish observed at a particular temperature when summed over an entire experiment. To compensate for this, prior to calculation of the mean and modal selected temperatures, we adjusted the data by using the number of fish per total occurrence of a particular temperature in all experimental compartments rather than the actual number of fish at each temperature.

We defined the "initial selected temperature" as that chosen by the fish immediately following establishment of a gradient of 10°C. The modal selected temperature was determined from the percent occurrence frequency distribution derived from adjusted data. After an initial time of apparent searching and testing of water conditions the experimental animals selected a temperature or range of temperatures at which they remained for the duration of the experiment. We called this the final selected temperature (or temperature range) and determined it from plots of selected temperature against time. The mean selected temperature was derived by methods presented in Appendix Table 1.

EXPERIMENTAL TECHNIQUES AND BEHAVIORAL RESPONSES

Our experimental techniques and data interpretation methods are useful for a wide variety of behavioral types. There are three salient features of this methodology: 1) the shifting and reversal of the temperature gradient to partition position preference from thermal preference, 2) the extended duration of the experimental period and its relationship to the thermal history of the test organisms, and 3) the criteria for behavior evaluation.

Shifting and Reversal of Temperature Gradient

Hasler (1956) pointed out that fishes in experimental gradients can position themselves according to small deformities in the tank structure. We employed two methods to eliminate this factor: shifting the position of a given isotherm in the gradient during an experiment, and reversing the hot and cold ends between replicate experiments.

Shifting the isotherm position during an experiment required the fish to thermoregulate actively, similar to those studied by Beitinger (1976, 1977) in his temporal gradient. This technique demonstrated that the fish could follow an isotherm and did not necessarily arbitrarily select a position in the experimental tank. The precision with which a group of fish followed an isotherm varied between species and was related to the size of their preferred temperature range. Juvenile surfperch, *Damalichthys vacca*, for example, which preferred a narrow range of temperatures, closely followed an isotherm (approximately 11°C) (Figure 3). In contrast, juvenile topsmelt, *Atherinops affinis*, after initially selecting approximately 22°C, remained within that compartment, and shifting the gradient did not cause them to move until the temperature reached 26°-27°C. This isotherm was then tracked (Figure 3). Topsmelt are physiologically eurythermal, at least during embryonic stages, and the upper limit for hatching of topsmelt eggs is 26.8°C (Hubbs 1965). Brett (1956) suggested that the preferred temperature may not be a strong enough directing force to move

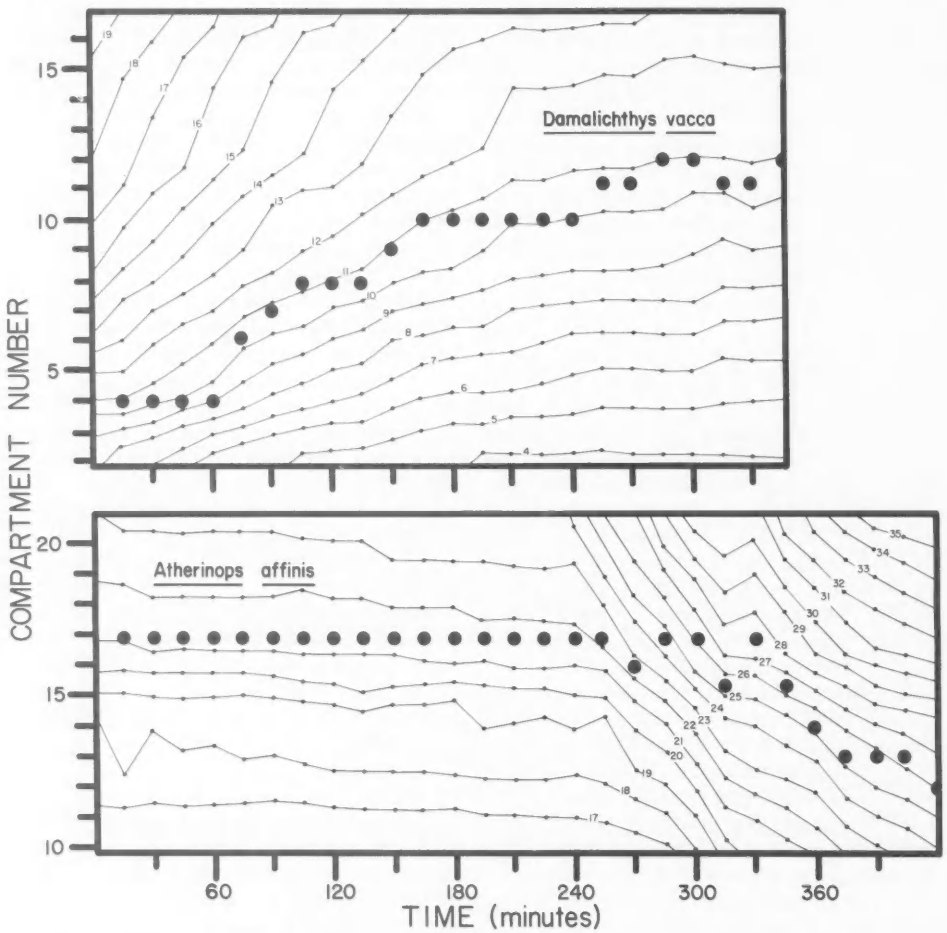

FIGURE 3.—Changes in fish and isotherm position in the experimental gradient. Juvenile *Damalichthys vacca* followed the 10°-11°C isotherms. Juvenile *Atherinops affinis* remained in the position they initially selected and moved very little until the temperature reached 26°-27°C. They then followed the temperature range of 25°-27°C. The small numbers indicate isotherms. Large dots indicate the mean temperature selected by nine individuals.

fish with wide temperature tolerances from a particular area until stress-inducing conditions are reached.

Temperatures Selected and Their Relationship to Thermal History

We classified the behavioral responses of the 16 species surveyed into four groups based on changes in temperatures selected throughout an experiment: 1) immediate response—no general shift in selected temperature over time, 2) fast response—a shift in selected temperature not exceeding the first 2 h of the run, 3) slow response—a shift in selected temperature over more than 2 h, and 4) positioned response—a broad preference and a tendency to remain in a given position in the gradient until conditions become extreme.

Shiner surfperch, *Cymatogaster aggregata*; pile surfperch, *Damalichthys vacca*; black surfperch, *Embiotoca jacksoni*; and black croaker, *Cheilotrema saturnum*, showed the first behavioral pattern of immediate response (Figure 4). These fishes moved most quickly from their preexperimental acclimation temperature to their final selected one or range, remaining there for the duration of the experiment. These fishes generally had the narrowest selected temperature ranges and also aggregated tightly (Table 1).

Fishes with a fast response to the temperature gradients included speckled sanddab, *Citharichthys stigmaeus*; señorita, *Oxyjulis californica*; spotted sand bass, *Paralabrax maculatofasciatus*; and sculpin *Scorpaena guttata* (Figure 5). These species required up to 2 h to home in on a selected temperature and also generally did not aggregate as tightly, nor select as narrow a temperature range as those fishes that showed an immediate response to the temperature gradients (Table 1).

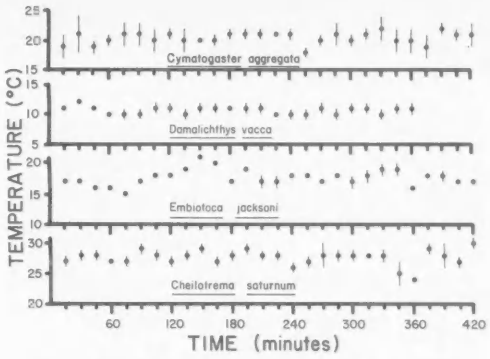

FIGURE 4.—Immediate response to temperature change. These species showed no trend in selected temperature with time. Dots are mean selected temperatures and vertical lines are 1 SD about the means. Results are for duration of one experiment.

All larvae studied responded slowly under experimental conditions. These included topsmelt, *Atherinops affinis*; California grunion, *Leuresthes tenuis*; rockpool blenny, *Hypsoblennius gilberti*; and painted greenling, *Oxylebius pictus* (Figure 6). Four older fishes also showed this behavior: kelp bass, *Paralabrax clathratus*; olive rockfish, *Sebastes serranoides*; California halibut, *Para-*

TABLE 1.—Behavioral responses of larval and juvenile fishes in temperature selection experiments. Initial and final selected temperatures are taken from Figures 4-6 and other similar experimental data.

Species	Experimental date	No. of fish	Mean Standard length (mm)	Mean Acclimation temperature (°C)	Selected temperatures (°C)					Coefficient of skewness (g_1)	Coefficient of kurtosis (g_2)	Coefficient of dispersion (%)
					Mean	SD	Mode	Initial	Final			
Immediate response:												
Cymatogaster aggregata	12 June 1975	8	109	18.2	19.9	2.1	19	18.7	21	0.22	2.87	24
Damalichthys vacca	6 June 1975	9	69	18.1	10.5	0.9	10	11.4	11	0.41	4.61*	12
Embiotoca jacksoni	13 Dec. 1974	7	118	16.7	18.0	1.6	18	17.0	18	−0.61*	4.54*	5
Cheilotrema saturnum	6 Oct. 1975	7	42	17.0	27.6	2.0	28	26.6	28	−0.79*	3.12	13
Fast response:												
Citharichthys stigmaeus	22 Dec. 1975	9	90	18.9	10.1	2.6	10	14.8	10	0.43	3.44	33
Oxyjulis californica	28 May 1975	6	120	17.2	15.5	1.9	15	15.0	16	−0.69*	5.44*	11
Paralabrax maculatofasciatus	31 July 1975	6	179	20.6	24.2	3.1	27	21.2	25	−0.83*	2.70	29
Scorpaena guttata	24 Nov. 1975	6	64	17.6	17.5	4.2	19	17.2	17	−0.63*	4.01*	35
Slow response:												
Atherinops affinis (larvae)	31 July 1975	6	14.5	21.5	25.2	2.9	27	21.9	27	−1.07*	4.12*	26
Leuresthes tenuis (larvae)	9 May 1975	6	8.1	16.5	25.2	4.1	26	19.2	27	−0.12	2.86	37
Hypsoblennius gilberti (larvae)	2 July 1975	6	4.4	19.4	22.2	3.1	19	19.7	26	0.39	2.10	36
Oxylebius pictus (larvae)	14 May 1975	6	3.4	16.0	26.8	3.3	27	19.7	29	0.82*	3.24	30
Paralabrax clathratus	28 July 1975	6	196	21.0	13.5	3.1	14	17.2	15	0.13	2.70	47
Sebastes serranoides	11 Dec. 1974	8	82	17.0	18.0	1.3	18	16.2	17	−0.21	2.44	4
Paralichthys californicus	15 Oct. 1975	5	94	20.5	20.8	6.6	24	20.3	22	−0.10	1.91*	65
Pleuronichthys coenosus	3 Dec. 1975	4	134	10.0	7.5	2.5	7	10.8	7	1.40*	5.15*	23
Positioned response:												
Atherinops affinis	14 Jan. 1976	9	60	15.0	23.3	3.2	26	16.4	26	−0.71*	2.41	4

*$P<0.05$.

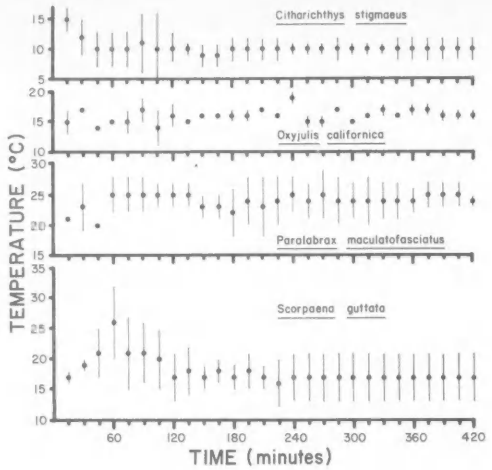

FIGURE 5.—Fast response to temperature change. These species changed their selected temperatures over the first 2 h of the experiment only. Symbols as in Figure 4.

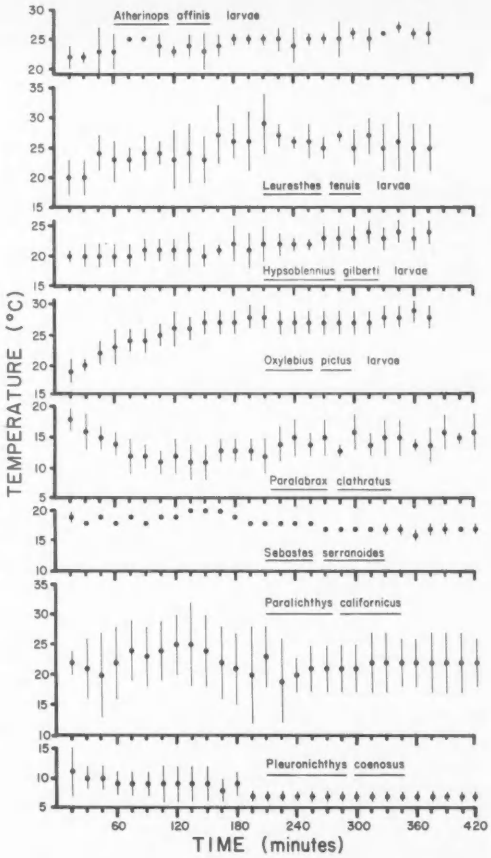

FIGURE 6.—Slow response to temperature change. These fishes changed their selected temperature over more than 2 h in the experiments. Symbols as in Figure 4.

lichthys californicus; and C-O turbot, *Pleuronichthys coenosus* (Figure 6). Members of this group required more time to stabilize their response than either the immediate or fast responders. The temperature selection acuity and aggregating tendencies of these fishes were similar to those of the second group (Table 1).

Juvenile topsmelt were the only species observed that showed a positioned response (Figure 3). Ehrlich et al. (in press) discussed this behavior in detail. California grunion are closely related to topsmelt, and we have observed them together, in the field, throughout larval, juvenile, and adult stages. Possibly juvenile California grunion, which were not tested, may show similar responses.

Preexperimental acclimation temperatures showed the greatest effect on thermal selection of the fishes during the first 2 h after establishment of the gradient (Figures 4-6). The short duration of the influence of thermal history on temperature selection has also been reported by Doudoroff (1938). Clearly, trying to determine a preferred temperature for these species or others with similar responses, during the transition period, would make data interpretation difficult. After this initial period, the fishes, in most cases, chose a final selected temperature, which may be synonymous with what Fry (1947) termed the "final preferendum." He defined this as the temperature range that the fish would eventually select, independent of their acclimation temperatures. Topsmelt, however, did not show this pattern, for their initial selected temperature gave a good indication of their preference and was independent of their acclimation temperature (Ehrlich et al. in press). Doudoroff (1938) also found that fishes did not select the temperatures to which they had been acclimated but rather selected a common range of temperatures, which he suggested must have some physiological significance.

Figures 4-6 show that the final preferendum was reached within several hours after the establishment of the gradient. This is considerably less time than the approximately 24 h reported by

Reynolds and Thomson (1974) or Reynolds and Casterlin (1976). The differential, however, between the acclimation and the final preferendum must be considered. Reynolds and Thomson (1974) tested fish acclimated 17°C below their final preferendum. Crawshaw (1975) used a range of acclimation temperatures from 22°C below to 3°C above the final preferendum and found that as the temperature differential diminished so did the time required to reach the final preferendum. Differentials of 5°C required as little as 1 h and 3°C only 0.5 h (Crawshaw 1975). Based on the temperature differences between acclimation and the final preferendum (Table 1), Reynolds' and our results generally fit the pattern described by Crawshaw.

Behavioral Criteria

Most studies pertaining to behavioral responses of fishes to thermal gradients have been concerned with only one factor: the final preferendum. Additional information, however, can be obtained from examination of parameters associated with the frequency distribution of the selected temperatures, particularly: skewness (degree of distortion from symmetry) and kurtosis (peakedness). Ivlev and Leizerovich (1960) compared the percent of the area under the curve of number of fish per temperature against the mode of the distribution as well as the percentage of the curve on either side of the mode. Reynolds and Casterlin (1976) and Reynolds (1977) discussed the relationship between various measures of central tendency (mean, mode, and median) and skewness. They also improved descriptions of thermal behavioral responses by quantifying skewness but did not state the statistical significance of the skewness. Sôkal and Rohlf (1969) stated that the absolute value of coefficients of skewness and kurtosis have little meaning and that they must be tested for statistical significance. We identified distinct behavioral types with respect to the frequency distribution of selected temperatures by examining skewness and kurtosis. The responses were, in part, species-specific but also varied with ontogenetic stage and nutritive condition. Reynolds and Casterlin (1976) showed that skewness also varied diurnally. Kurtosis can be used to assess whether the test organisms display eury- or stenothermal behavioral responses (Ivlev and Leizerovich 1960). A narrow preferred temperature range will be overly peaked about the mean (leptokurtic), and a broad range of preferred temperatures will show no obvious mode or only a very slight one (platykurtic). The coefficient of kurtosis is particularly useful for quantifying the strength of the temperature selection response in populations that are not normally distributed where normal parameters such as mean and standard deviations are inappropriate.

A normal bell-shaped frequency distribution is representative of species with a wide preferred temperature range that is not close to lethal or avoided temperatures. Speckled sanddabs displayed this type of behavior (Table 1, Figure 7). Newly hatched larvae, however, of species such as California grunion showed little temperature selection acuity and preferred an even wider range of temperatures ($g_1 = 0.003$, $0.5<P$), ($g_2 = 1.75$, $0.01<P<0.025$). This behavior resulted in a platykurtic distribution (Figure 7). Reynolds and Thomson (1974) reported that newly hatched Gulf grunion, *Leuresthes sardina*, also showed no acute temperature preference. The precision with which larval California grunion selected temperatures increased by 2 days posthatching, producing a

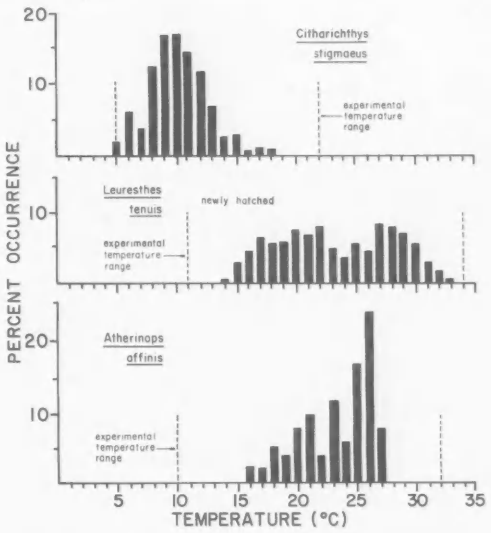

FIGURE 7.—Temperature-specific occurrences. Examples of three types of frequency distributions: normal (based on 220 fish observations), adult speckled sanddabs; platykurtic (based on 281 fish observations), newly hatched California grunion; and, skewed to the left (based on 241 fish observations), juvenile topsmelt.

normal frequency distribution (Table 1), but subsequent food deprivation resulted in selection of colder water (mean 18.7°C) and a narrower distribution (SD 3.3°C). Selection of colder water during food deprivation may be a mechanism of energy conservation by poikilothermic organisms. Other mechanisms of energy conservation, both behavioral and biochemical, have been found during starvation of herring and plaice larvae (Blaxter and Ehrlich 1974; Ehrlich 1974). The increased precision of temperature selection during food deprivation coincides with the findings of Reynolds (1977) that stress can increase precision of temperature selection. This pattern, however, of lowered selected temperature but increased precision during food deprivation was not duplicated by all species.

Comparison of data from 2 consecutive days of observation of shiner surfperch demonstrated that the temperatures they selected, as well as their tendency to school or aggregate, varied between the 2 days. The selected temperatures decreased on the second day (means 19.9° to 15.6°C and modes 19° to 16°C), but unlike California grunion the standard deviation of the mean increased (2.1° to 2.6°C). School tightness also decreased as indicated by a larger coefficient of dispersion (24 to 37%). The major preexperimental difference between the first and second day runs was that the fish were not fed before the second day of experimentation. The lowering of the preferred temperature during food deprivation followed that of the California grunion and brook trout (Javaid and Anderson 1967). Furthermore, this selection of cooler water during food deprivation agrees with the findings of Brett et al. (1969) and Brett and Higgs (1970) who showed that a limited food supply resulted in a decrease in the optimal temperature for growth, which is coincident with the final preferendum for sockeye salmon (Brett 1971). The wider preferred temperature range and reduced aggregation may reflect increased searching by hungry fish. Hunger can cause fish to increase the distance between individuals (Hunter 1965) as well as disrupt fish school integrity (Blaxter and Holliday 1958).

Larval California grunion, topsmelt, rockpool blennies, and painted greenlings selected water that was often warmer than naturally available. This behavior has several adaptive advantages but also presents potential harmful consequences resulting from man's alteration of their natural habitat. Selection of warm water by larvae will reduce the duration of the highly vulnerable yolk-sac and larval stages. In King Harbor it kept many of these larvae in the back basins that contained the largest concentration of food organisms (McGowen[5]). Furthermore, in genera such as *Hypsoblennius* that become demersal following the planktonic larval stages, selection of warm water will help the larvae to remain in the nearshore environment where they must be when they leave the planktonic community. Marshall (1966) discussed similar mechanisms by which nearshore demersal species maintain their population integrity. Rockpool blenny larvae, however, that entered water warmer than 28°C lost their equilibrium, could not extricate themselves and eventually died. This same behavioral response of entering water above a lethal temperature and not leaving it has been reported for other species (e.g., Beitinger and Magnuson 1976). Similar behavior in the field near sources of hot water such as power plant effluents may significantly affect local populations. This could be magnified as a result of predation, for it has been shown that the vulnerability of fishes to predation is increased by sublethal heat shocks (Sylvester 1972; Coutant 1973; Yocum and Edsall 1974).

Various workers (Lowe and Heath 1969; Reynolds and Thomson 1974; Reynolds and Casterlin 1976; Beitinger 1977) have reported that the final preferendum is often close to the upper lethal temperature. Frequency distributions skewed to the left such as for topsmelt (Table 1, Figure 7) are reflective of this behavior. The mode occurrence for topsmelt was 26°C, and they sharply avoided warmer water. Coutant (1975) pointed out that the upper avoidance temperature is more sharply defined than the lower one for most species. Beitinger (1977) found bluegill, *Lepomis macrochirus*, tolerated less variation in avoidance temperature near their lethal limits.

Differences in group cohesion for individual runs between nonschooling species such as adult speckled sanddabs (Figure 5) and tightly aggregating ones such as olive rockfish (Figure 6) are illustrated by comparison of the standard deviations about the run selected temperatures. Although a low coefficient of dispersion may indi-

[5]McGowen, G. E. 1977. Effects of thermal effluent from Southern California Edison's Redondo Beach Steam Generating Plant on the warm temperate fish fauna of King Harbor marina. Ichthyoplankton study report for Phase II. Annual Report for 1 March 1975-29 February 1976. Unpubl. manuscr., 46 p. Southern California Edison Res. Contract No. U0654902.

cate tighter aggregation, it could also result from individuals of a normally solitary species with a narrow preferred temperature range being compressed into a tight aggregation by a steep temperature gradient. Comparison of the coefficient of dispersion and the measures of eury- or stenothermal preference (the standard deviation about the mean selected temperature and the coefficient of kurtosis) (Table 1) helps to distinguish between behavioral aggregation and compression of individuals with stenothermal preferences. Juvenile topsmelt, for instance, aggregated closely, but the close association of the individual fish was not the result of thermal compression since they showed a wide temperature preference (Table 1). Greater caution, however, must be used in interpreting the coefficient of dispersion for species such as pile surfperch with a narrow (leptokurtic) range of preferred temperatures (Table 1). The occurrence of pile surfperch in the field at temperatures of 12°-18°C (Stephens[6]) shows that the close aggregation in the gradient was not due to thermal compaction of fish with an obligatory stenothermal preference. These fish in King Harbor were associated with the coolest water available (Stephens, see footnote 6). Coordinated laboratory and field studies provide greater understanding of the factors that affect fish populations and distributions than either investigation alone.

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[6]Stephens, J. 1977. Effects of thermal effluent from Southern California Edison's Redondo Beach Steam Generating Plant on the warm temperate fish fauna of King Harbor marina. Field study report for Phase II. Annual Report for 1 March 1975-29 February 1976. Unpubl. manuscr., 111 p. Southern California Edison Res. Contract No. U0654902.

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APPENDIX TABLE 1.—Equations and an example from an artificial data set for calculation of mean selected temperature and coefficient of dispersion. An artificial data set was used to provide a more concise presentation of the mathematical techniques. The standard deviation of the mean selected temperature is 0.7°C, and the data are neither significantly skewed ($g_1 = 0.00$, $P>0.05$) nor lepto- or platykurtic ($g_2 = 2.5$, $0.2<P<0.4$). Initial, mean, modal, and final selected temperatures were equal (13°C).

MEAN SELECTED TEMPERATURE (MST)

METHOD	EQUATIONS	EXAMPLE
STEP 1. Eliminate individual fish observations at the extreme ends of the gradient.		Eliminate the one fish that occurred in Compartment 1 at 075 min (see Artificial Data Set).
STEP 2. Determine the frequency of occurrence of individual temperatures $f(T_i)$ and the number of fish (F_i) at each temperature (T_i).	$i = 1,\ldots,n$ T_1 = minimum observed temperature T_n = maximum observed temperature	See Data Analyses for Artificial Data Set.
STEP 3. Define the valid experimental range (R) as the continuous interval in which the minimum occurrence of a temperature is at least 25% of the maximum observed temperature frequency.		R = 8-16°C (See Data Analyses for Artificial Data Set.)
STEP 4. When $T_i \varepsilon R$ ($\bar{T}_i \varepsilon R$), calculate the relative number of fish (f_i) corrected for the variation in occurrence of each temperature.	$f_i = \dfrac{F_i}{f(T_i)}$	See Data Analyses for Artificial Data Set.
STEP 5. When $T_i \varepsilon R$, calculate the corrected number of fish (f') for the range of temperatures (R) analyzed.	$f' = \sum_{i=1}^{n} f_i$	f' = 4.97 (See Data Analyses for Artificial Data Set.)
STEP 6. Compute the percent occurrence of fish (P_i) for each $T_i \varepsilon R$.	$P_i = \dfrac{f_i}{f'} \times 100$	See Data Analyses for Artificial Data Set.
STEP 7. Determine the mean selected temperature (MST), when $T_i \varepsilon R$.	$MST = \sum_{i=1}^{n} P_i/100 T_i$	MST = (0.20)(12°C) + (0.60)(13°C) + (0.20)(14°C) = 13.0°C (See Data Analyses for Artificial Data Set.)

COEFFICIENT OF DISPERSION (CD)

METHOD

First calculate the coefficient of dispersion for an individual run (cd_j) and then for the entire experiment (CD).

EQUATIONS

$$cd_j = \frac{2\,sd_j}{T_{jmax} - T_{jmin}} \times 100$$

where

$j = 1,\ldots,m$

m = number of experimental runs

sd_j = standard deviation of the run selected temperature of the j^{th} run

T_{jmax} = maximum experimental temperature of the j^{th} run

T_{jmin} = minimum experimental temperature of the j^{th} run

$$CD = \frac{\sum_{j=1}^{m} cd_j}{m}$$

EXAMPLE

$$cd_{000\ min} = \frac{(2)(0.9^{\circ}C)}{15^{\circ}C - 5^{\circ}C} \times 100 = 18\% \qquad CD = \frac{(10)(18\%)}{10} = 18\%$$

(See Artificial Data Set.)

DATA ANALYSES FOR ARTIFICIAL DATA SET

i	$\bar{T}_i$ (°C)	$f(T_i)$	F_i	f_i	P_i
1	5	1	0	–	–
2	6	7	0	–	–
3	7	5	0	–	–
4	8	19	0	0	0
5	9	9	0	0	0
6	10	29	0	0	0
7	11	10	0	0	0
8	12	30	29	0.97	20%
9	13	10	30	1.00	60%
10	14	30	30	1.00	20%
11	15	10	0	0	0
12	16	25	0	0	0
13	17	7	0	–	–
14	18	13	0	–	–
15	19	3	0	–	–
16	20	2	0	–	–
				$\Sigma f_i = 4.97 = f'$	

R

ARTIFICIAL DATA SET

TIME (min)	COMPARTMENTS 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	RUN SELECTED TEMP.(°C) MEAN	SD	cd (%)
000																								
TEMP. (°C)	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0			
NO. OF FISH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	13.0	0.9	18
015																								
TEMP. (°C)	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0			
NO. OF FISH	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	13.0	0.9	18
030																								
TEMP. (°C)	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0			
NO. OF FISH	0	0	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	13.0	0.9	18
045																								
TEMP. (°C)	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0			
NO. OF FISH	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	0	0	13.0	0.9	18
060																								
TEMP. (°C)	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0	18.5	19.0			
NO. OF FISH	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	0	0	0	0	13.0	0.9	18
075																								
TEMP. (°C)	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0	18.5	19.0	19.5	20.0			
NO. OF FISH	1	0	0	0	0	2	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	13.0	0.9	18
090																								
TEMP. (°C)	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0	18.5	19.0			
NO. OF FISH	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	0	0	0	0	13.0	0.9	18
105																								
TEMP. (°C)	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0			
NO. OF FISH	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	0	0	13.0	0.9	18
120																								
TEMP. (°C)	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0			
NO. OF FISH	0	0	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	0	0	13.0	0.9	18
135																								
TEMP. (°C)	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0			
NO. OF FISH	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3	2	1	0	0	0	0	13.0	0.9	18

LINEAR PROGRAMMING SIMULATIONS OF THE EFFECTS OF BYCATCH ON THE MANAGEMENT OF MIXED SPECIES FISHERIES OFF THE NORTHEASTERN COAST OF THE UNITED STATES

B. E. BROWN, J. A. BRENNAN, AND J. E. PALMER[1]

ABSTRACT

We evaluated the results of using historic bycatch (incidental catch) ratios in adjusting fishing regulations by linear programming techniques. We used both 1971 and 1973 bycatch ratios separately to assess the sensitivity of the results to the reported changes in bycatch ratios in estimating the total 1975 catch of countries fishing in the northwest Atlantic. For 4 of the 11 countries for which data were examined, the difference between the percentage of a country's species total allowable catches (i.e., those catches allowed a country by regulation) using the 1971 and 1973 bycatch ratios, was at least 20%. Only four countries were predicted to catch at least 80% of their species total allowable catches. The predicted total catches of all countries and all species was only 60% of the total species quotas. The simulated directed fisheries constituted only 70% of the total catch using 1971 bycatch ratios and only 73% using 1973 bycatch ratios. Examination of the reported 1975 catches indicated that the total allowable catches for herring were most frequently limiting a country's catch. Except for U.S.S.R., the differences between reported and simulated catches were less than 50 metric tons, with the difference less than 10 metric tons for 6 of the 11 countries. There was little difference in reported versus simulated catches between the schemes using the 1971 and 1973 bycatch ratios.

The control of fishing mortality by means of individual species catch quotas is difficult in a mixed fishery, i.e., where a significant proportion of the fishing mortality on a given species is generated as a result of the incidental catch, or bycatch, of that species in fisheries directed toward other species. Moreover, if a country is allowed to catch a specified amount of a given species by means of a directed fishery for that species, the total species catch may exceed that amount because of the associated bycatch of that species in the other fisheries.

The International Commission for the Northwest Atlantic Fisheries (ICNAF) modified its regulatory measures several times in attempts to account for bycatches of species under quota restrictions. The initial haddock quota regulations (Subarea 5 and Division 4X, Figure 1) stated that the directed fishery should cease when the accumulated catch (directed catch plus bycatch) reported to ICNAF biweekly reached 80% of the quota, anticipating that the catch after closure (a bycatch by definition) would be 20% of the quota (ICNAF 1969). When yellowtail flounder was added to the list of species under quota, the closure procedures were changed. The Assessments Subcommittee of ICNAF estimated the expected monthly bycatch after closure of directed fisheries and the decision to cease directed fishing was then made when the accumulated total catch reported to ICNAF on a biweekly basis plus the expected bycatch during the remainder of the year equalled the quota (ICNAF 1970). With the introduction of national quota allocations in 1972, the procedure again changed, requiring each country to control its directed fishery so that the sum of its directed catch and the estimated bycatches would not exceed its quota allocation (ICNAF 1972a).

The bycatch problem was acknowledged by ICNAF in its decision to establish a TAC (total allowable catch, i.e., that catch allowed a country by regulation) for all species combined that was less than the sum of the individual species TAC's for 1974 and 1975 (ICNAF 1974a). Linear programming simulations utilizing bycatch ratios from directed fisheries for all countries combined substantiated this policy (Brown et al. 1973; Anthony and Brennan 1974).

Since 1974, TAC's were set for all species (either singly or in groups) and for national catches (ICNAF 1974a, 1975a). Under this regime, it was possible to utilize linear programming more realistically to investigate the extent to which the

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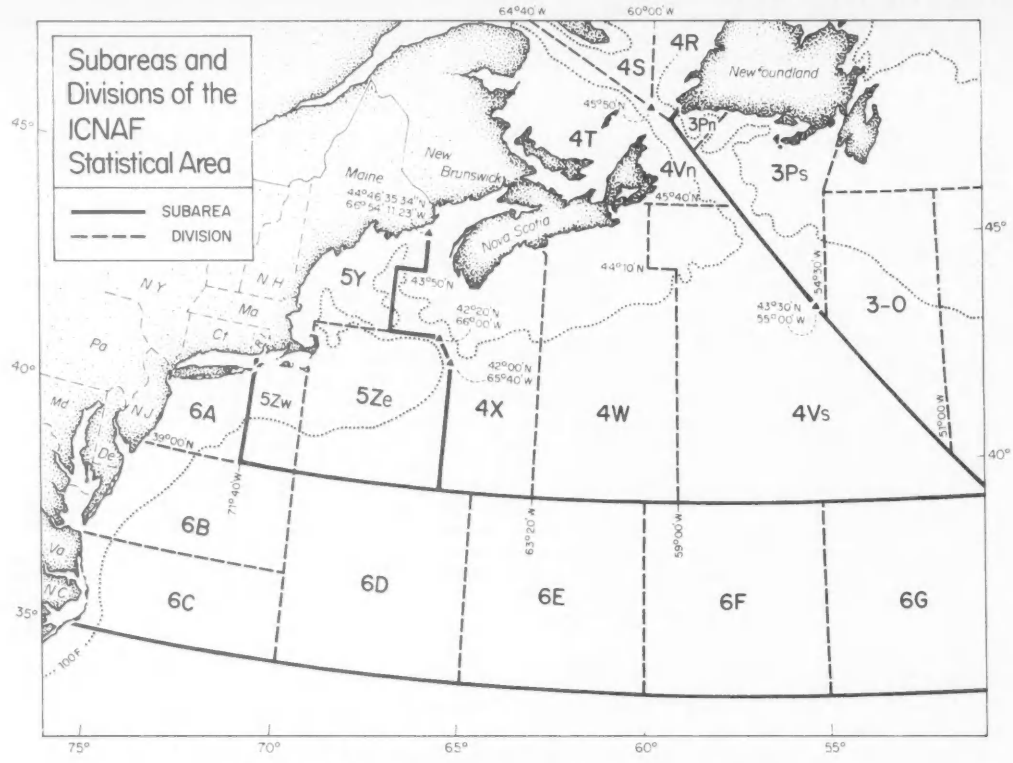

FIGURE 1.—Northwest Atlantic Ocean partitioned into ICNAF areas.

regulations in ICNAF were adequate to account for the bycatch. Simulations of 1975 catches were made utilizing bycatch ratios from both 1971 and 1973 to assess the sensitivity of the technique to differences in historic bycatch ratios. Brennan (1975) found little evidence of a decline in bycatch ratios when examined on a country-gear level over the years 1970-73. We compared the simulated catches and the reported catches on a species basis and on a country basis and examined the results to determine for which countries and species the simulations were successful.

METHODS AND MATERIALS

Data Base

Almost all countries fishing in Subarea 5 and Statistical Area 6 (Figure 1) submitted data on nominal catch (i.e., that reported landed (adjusted to live weight) by the country, not necessarily that actually caught—it is the term used in the ICNAF Statistical Records following standard United Nations Food and Agricultural Organization procedures) and effort for main species (or a species) sought. These data are published each year in tables 4 and 5 in the annual ICNAF Statistical Bulletins. The data of 1971 and 1973 (ICNAF 1972b, 1975b) were the sources of the bycatch ratios. Data of these years were reported according to the species categories given in Table 1. The nominal catches do not include fish caught and discarded at sea.

The nominal catch and effort (days fished) for 1971 and 1973 for finfish were summed over months for each target fish of the fishery (the "main species sought") categories reported in tables 4 and 5 of the ICNAF Statistical Bulletin (1972b and 1975b, respectively). Catches made with fixed gear as well as catches of Atlantic menhaden, Atlantic halibut, and large pelagic fishes, i.e., tunas, billfishes, and sharks (other

than dogfishes), were excluded. Most of these were not covered by the regulations and have <1 t (metric ton) per 100 t of directed species caught. In instances where no "main species sought" category was indicated or where landings were attributed to a mixed fishery, the monthly landings by vessel classification and gear were assigned to "species sought" categories according to the species which formed a simple plurality of the catch. The United States of America often reported mixed fisheries on groundfish species. The Union of Soviet Socialist Republics (U.S.S.R.), Poland, Japan, and German Democratic Republic (G.D.R. ypically reported their pelagic and/or squid f ery catches as mixed.

The term "fishery" as used in this paper re to the vessels and associated catch on these "main species sought" categories. The term "species" refers to both individual species and species groups. All reported landings were thus identified by two factors: species and fisheries. Such tabulations were prepared for all nations for which data were available. For Romania, which has had an Atlantic herring fishery but did not report a directed Atlantic herring fishery in 1973, bycatch ratios for 1972 (ICNAF 1974b) were used for that species fishery. The only countries with an allocated national quota for which 1971 and 1973 data were not available and thus could not be analyzed were Italy (1971 and 1973) and France (1971).

In this paper, all catch restrictions described below will all be referred to as "quotas." To apply linear programming techniques to the bycatch problems restraints on the total catches for each species by country need to be set. For countries and for species categories reported in ICNAF Statistical Bulletins, we used restraints in linear programming (ICNAF 1974a). For countries and/or species for which ICNAF had not set specific quota allocations (but for which the quota was included in, say, "other countries" under ICNAF regulations—a country not given a specific catch quota could fish in competition with other similar countries from an "other country" allocation or "other flounder" category), we estimated these restraints by the following procedures. These were chosen so that the categories of quota allocations matched the species categories (Table 1) by which the catches were reported. We proportioned the "others" allocation category for each individual species to countries based on the 1973 nominal catch for each particular species and the catch of that species of all of the countries that did not have a national quota for the species. We proportioned the quota for "other groundfish" and "other pelagic" from the "other fish" TAC for each country. The quotas for American plaice and witch flounder were subtracted from the "other flounder" TAC for each individual country. Since the quota for pollock was set by ICNAF for Division 4VWX plus Subarea 5, national quota allocations were estimated as an average percent of the nominal pollock catches during 1971, 1972, and 1973 in Subarea 4VW and 5.

TABLE 1.—Species categories as reported to ICNAF, 1971 and 1973.

1971	1973	1973
Atlantic cod	Atlantic cod	Yellowtail flounder
Haddock	Haddock	Other flounder
Redfish	Redfish	Atlantic herring
Atlantic halibut	Silver hake	Atlantic mackerel
Silver hake	Red hake	Other pelagic
Atlantic herring	Pollock	Other groundfish
Other pelagic	American plaice	Other fish
Other groundfish	Witch flounder	Squids
Other fish plus squids		

Analysis Methods

Linear programming is a optimization method for which the effectiveness of an allocation scheme distributed over several variables is measured by the maximum or minimum value of some linear function of those variables, when those variables are subject to linear constraints. The problem considered here was to determine $X = (x_1, x_2, \ldots, x_n)$ such that

$$z = \sum_{i=1}^{n} c_i x_i \qquad (1)$$

is maximized, where for each i, c_i was the weighting coefficients of the variable x_i. In the present context,

x_i = catch of species i to be taken in directed fishery for species i,

c_i = catch of species i in all fisheries divided by catch of species i taken in directed fishery for species i ($c_i \geq 1.00$),

n = number of directed fisheries considered, and

z = total catch of all species.

Solutions $(x_1, x_2, \ldots, x_n)$ of Equation (1) were subject to the constraints for each i

$$\sum_{i=1}^{n} \hat{a}_{ij} x_i \leq b_j \qquad (2)$$

$$x_i \geq 0 \qquad (3)$$

where $\hat{a}_{ij}$ = catch of species j taken in directed fishery for species i/catch of species i in directed fishery for species i

b_j = constraint on total catch of species j, for $j = 1 \ldots m$.

The estimates of $\hat{a}_{ij}$ for each country for 1973 are presented in Appendix Table 1. Analogous tables for the 1971 data are in Brown et al. (1973).

The solution used in this paper was devised by using the Simplex Algorithm (Hadley 1963:132f) which was computed by using a Honeywell[2] computer program LINPRO; a description of this use of linear programming is given in appendix II of Brown et al. (1973). In this analysis the linear constraints were that no country would exceed its national allocation for any species (b_j). The output of the LINPRO program includes the vector X of directed catches of the species along with the resultant total catches of the species and the overall total catch.

RESULTS AND DISCUSSION

The results of each country's simulation are given in Appendix Table 2. In each case the sum of the species quota allocations exceeded the country's maximum possible catch (without violating single species constraints) as determined by the linear programming model. Table 2 lists the ratios of the simulated catches to the TAC's using 1973 and 1971 bycatch ratios. For 4 countries (Bulgaria, Canada, G.D.R., and Japan) of the 11, the percentages derived from 1971 bycatch ratios differed from those derived from 1973 fishing patterns by at least 0.20. More detailed reporting of catches (i.e., by species rather than groups) in 1973 than in 1971 and, therefore, in the analysis contributed to this change. Poland, United States, France, and Federal Republic of Germany (F.R.G.) were the only countries which could have taken >80% of the sum of their species TAC's based on 1971 or 1973 bycatch rates. The United States, however, has a significant discard of fish which is not taken into consideration in this analysis. Of the other countries considered, the effect of unreported discard would be expected to be greatest in the Spanish squid fisheries.

TABLE 2.—Comparison of maximum catches from linear programming simulation using 1971 and 1973 bycatch ratios, with sum of species "quotas" for the ICNAF area.

Country	Maximum catch—sum of species quota using: 1973 bycatch ratios	1971 bycatch ratios
Bulgaria	0.64	0.83
Canada	.54	.78
France	.52	—
Federal Republic of Germany	.97	.82
German Democratic Republic	.40	.64
Japan	.57	.17
Poland	.94	.93
Romania	.08	.05
Spain	.72	.72
U.S.S.R.	.25	.35
United States	.90	.93

Closer inspection of Appendix Tables 2 and 3 reveals the species which were the limiting factors in a country's inability to take the sum of its species quotas at present. These are the species which were caught in significant amounts as bycatch and directed catch and for which a species quota was met. The species whose catch was most frequently limiting was herring, when either 1971 or 1973 bycatch ratios was used. The next major species using 1973 ratios were pollock and "other pelagic" and using 1971 ratios were "other fish," "other pelagic," and haddock. Pollock was less limiting when 1971 ratios were used because it was combined with the "other groundfish" category, which had not been limiting.

The sum of the linear programming estimates over countries using 1971 and 1973 data are presented in Tables 3 and 4, respectively. In each case the sum of the expected maximum catches determined by the linear programming runs was only about 60% of the sum of the species quota. The simulated directed fisheries catch levels composed only 70% using 1971 bycatch ratios and 73% of the

TABLE 3.—Sum of individual country's linear programming simulation of 1975 catches in the ICNAF area, maximizing total catch (1,000 t) and using 1971 bycatch ratios. Catches of France assumed to be those using 1973 bycatch ratios.

Species sought	Total allowable catch restraint	Directed catch	Total catch
Atlantic cod	45.00	1.7	18.53
Haddock	6.00	0.0	5.23
Redfish	25.00	6.60	22.20
Silver hake	175.00	43.65	62.68
Flounders	41.00	1.32	36.25
Other groundfish	152.00	64.08	84.49
Atlantic herring	175.00	140.14	176.69
Other pelagic	311.90	189.07	210.48
Other fish plus squids	127.40	26.08	67.25
Total	1,058.30	482.64	683.81

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 4.—Sum of individual country's linear programming simulation of 1975 catches, maximizing total catch (1,000 t), and using 1973 bycatch ratios for the ICNAF area.

Species sought	Total allowable catch restraint	Directed catch	Total catch
Atlantic cod	45.00	16.39	31.48
Haddock	6.00	0.00	5.25
Redfish	25.00	18.24	22.25
Silver hake	175.00	74.69	85.72
Red hake	65.00	11.83	26.51
Pollock	21.30	9.57	20.28
American plaice	2.70	—	1.15
Witch flounder	4.30	—	1.70
Yellowtail flounder	16.00	11.02	15.06
Other flounder	18.00	—	6.54
Other groundfish	65.70	27.38	40.96
Atlantic herring	175.00	107.38	120.01
Atlantic mackerel	285.00	127.51	150.60
Other pelagic	26.90	16.97	26.45
Other fish	56.40	9.33	33.35
Squids	71.00	25.93	40.30
Total	1,058.30	456.24	626.75

total using 1973 bycatch ratios, the rest being taken as bycatch. The highest percentage of TAC's, which were caught in directed fisheries, were for other pelagics (90%), Atlantic herring (79%), other groundfish (76%), and redfish (75%) using 1971 bycatch ratios, and for Atlantic herring (89%), silver hake (87%), Atlantic mackerel (85%), and redfish (82%) using 1973 bycatch ratios.

Referring to the individual country linear programming output tables in the Appendix, it is obvious that under 1971 and 1973 bycatch ratios, national patterns ran the gamut from almost a total mixed fishery by the U.S.S.R., and to a somewhat lesser extent by the G.D.R., to very specific fisheries of the F.R.G. and Poland.

As noted earlier, the species which was most frequently limiting to the total reported 1975 catch was Atlantic herring (6 out of 11 countries), and the countries which had the most limiting species TAC's were United States (5) and U.S.S.R. (4). Except for the catches of U.S.S.R., United States, G.D.R., and Poland, there was little difference in reported total catch minus simulated reported catch, when 1971 and 1973 bycatch ratios were used. Moreover, only for U.S.S.R were these differences $> 50{,}000$ t, and for six of the countries the differences were $< 10{,}000$ t for both schemes. The species for which the simulated and reported total catches differed most varied by country. Atlantic herring and Atlantic mackerel were the species most frequently differing in simulated vs. reported catches, but Atlantic mackerel and silver hake contributed most in metric tons to the differences. In general, and in view of the findings of Brennan (1975), the differences between schemes using 1971 and 1973 bycatch ratios were minimal, and more likely due to the different grouping of the data.

A summary of the 1975 TAC's, the 1975 reported catches, and the linear program estimates of total catch by country, is presented in Table 5. It is obvious that the overall TAC of 850,000 t for 1975 would not be attained without exceeding certain species TAC's unless bycatch was reduced, according to the simulations. The expected catches of 626,750 t using 1973 bycatch ratios and of 681,050 t using 1971 bycatch ratios are only 74% and 80%, respectively, of the 1975 total TAC. On a country basis, and using the results derived from the 1973 bycatches, it can be seen that the country total TAC's were set for 1975 at approximately appropriate levels for France and Spain (based on

TABLE 5.—Comparison of linear programming estimates of maximum total catch by overall country's total allowable catches (TAC's) in the ICNAF area. Figures in 1,000 t.

Country	1973 nominal catch of species regulated by the total TAC	Sum of species TAC's for 1975	1975 total TAC	Linear programming estimate of total catch		Actual 1975 nominal catch of species regulated on total TAC
				1973 bycatch ratios	1971 bycatch ratios	
Bulgaria	37.29	34.40	24.65	22.22	28.74	24.69
Canada	16.80	26.32	26.00	14.24	20.51	14.00
France	3.62	5.29	2.95	2.76	2.76	3.36
Federal Republic of Germany	38.28	30.89	24.85	30.05	25.31	25.10
German Democratic Republic	150.85	100.98	82.85	40.52	64.17	82.74
Italy	3.92		4.15	[1]	[1]	4.40
Japan	32.90	45.35	21.25	26.05	7.59	20.84
Poland	190.55	153.94	129.25	144.87	144.37	127.05
Romania	7.14	5.71	3.85	0.46	0.27	1.80
Spain	22.20	20.98	14.80	15.06	15.10	14.65
U.S.S.R.	449.04	366.64	301.80	93.10	127.02	313.78
United States	203.09	262.37	211.60	237.42	245.21	221.04
Total	1,155.68	[2]1,052.87	[3]850.00	626.75	[4]681.05	853.45

[1]No estimate available.
[2]Six thousand metric tons of other species not prorated to other species.
[3]Includes 2,000 t allocated to others.
[4]Due to the absence of bycatch ratios for 1971 data, estimate of France's total catch is derived from the 1973 bycatch ratios.

reported statistics), too low for the F.R.G., Japan, Poland, and United States, and too high for the other countries. In fact, summing the national total TAC's rather than the linear program estimates of country catch, when the former are limiting, to obtain an overall estimated catch, results in an expected total catch of 575,000 t, only 68% of the overall TAC. The analogous expected total catch derived from 1971 bycatch ratios was 627,470 t, only 74% of the overall TAC. Bycatch may be reduced through actions initiated by fishing fleets or by regulations such as the closure to bottom trawling by larger vessels in the southern New England, Middle Atlantic, and Georges Bank areas (ICNAF 1975) for 1975 and by the similar closure on Georges Bank for 1976. The reduction of the overall TAC to 650,000 t in 1976 (ICNAF 1976) and 525,000 t in 1977 (ICNAF 1977) was designed to reduce the bycatch problem.

It should be noted, however, that despite the above potential for change as well as the inadequacies of the reporting to ICNAF, which may combine more than one directed fishery under a mixed category, there were other factors which worked in the opposite direction. The first was the inadequate recording of bycatch noted during international inspections. Some of this was discarded and not reported, and some was apparently utilized but not accurately reported on logbooks. Both the lack of reporting and any underestimates of bycatch can cause the bycatch ratios used in this analysis to be underestimated.

In mixed species fisheries, bycatch must be considered in the allocation of quotas to species and to elements of the fishery (in this example the elements are countries, but under different circumstances they could be otherwise—e.g., ports). Lack of attention to attendant bycatch may result in an unexpected overharvest of selected species or conversely the wastage of large quantities of protein depending on whether or not the directed fishery ceased when a small amount of bycatch had been taken. Linear programming provides a suitable technique for examing this problem. However, to have a refined analysis, accurate statistics as to main species sought and the composition of the bycatch including discards must be available. Lacking these, the inferences as in this paper, are directional. The specific individual estimates can be interpreted for policy decisions only when the user has the understanding of the fishery to qualitatively account for the appropriate reporting inadequacies.

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APPENDIX TABLE 1.—1973 nominal landings by country (ICNAF Subarea 5 and Statistical Area 6), expressed as ratios of bycatch to main species sought within fisheries. See text for explanation.

	Species caught															
Species sought	Atlantic cod	Haddock	Redfish	Silver hake	Red hake	Pollock	American plaice	Witch flounder	Yellowtail flounder	Other flounders	Other groundfish	Atlantic herring	Atlantic mackerel	Other pelagic	Other fish	Squids
BULGARIA																
Herring	0.006	—	0.064	0.060	0.050	—	—	—	0.010	—	—	1.000	0.243	0.049	—	—
Mackerel	0.001	—	—	0.048	0.011	—	—	—	0.003	—	0.007	0.039	1.000	0.007	0.026	0.013
CANADA																
Cod	1.000	0.214	0.009	—	—	0.081	0.003	0.002	0.004	0.011	0.125	—	—	—	—	—
Haddock	0.549	1.000	0.002	—	—	0.126	0.015	0.004	0.001	0.004	0.059	—	—	—	—	—
Other groundfish	1.087	0.700	0.027	—	—	3.472	0.012	0.005	—	0.019	1.000	—	—	—	—	—
Herring	—	—	—	—	—	—	—	—	—	—	—	1.000	0.006	—	—	—
Other pelagic	—	—	—	—	—	—	—	—	—	—	—	—	—	1.000	—	—
FRANCE																
Atlantic herring	—	—	—	—	—	—	—	—	—	—	—	1.000	—	—	—	—
Squids	—	—	—	—	—	—	—	—	—	—	0.023	—	—	—	—	1.000
FEDERAL REPUBLIC OF GERMANY																
Pollock	0.005	—	—	0.027	—	1.000	—	—	—	—	0.065	—	—	—	—	—
Other groundfish	—	—	—	—	—	—	—	—	—	—	1.000	—	0.083	—	—	0.500
Atlantic herring	—	—	—	—	—	—	—	—	—	—	—	1.000	0.010	0.008	0.010	—
Atlantic mackerel	—	—	—	—	—	—	—	—	—	—	—	—	1.000	0.094	—	0.080
Squids	—	—	—	0.001	—	—	—	—	—	—	0.463	—	0.178	0.084	0.005	1.000
GERMAN DEMOCRATIC REPUBLIC																
Pollock	0.004	—	0.002	—	—	1.000	—	—	—	—	—	0.042	0.009	—	—	—
Atlantic herring	0.001	—	0.001	0.003	—	0.001	—	—	—	—	—	1.000	0.008	—	0.211	0.005
Atlantic mackerel	—	—	—	0.001	—	—	—	—	—	—	—	0.031	1.000	0.003	0.010	—
Other fish	0.011	—	—	0.006	—	0.006	—	—	—	—	0.001	0.204	0.225	0.006	1.000	—
JAPAN																
Other groundfish	—	—	—	—	—	—	—	—	—	0.044	1.000	—	—	—	—	0.067
Atlantic herring	—	—	0.015	0.011	—	—	—	—	—	0.001	—	1.000	—	0.057	0.038	0.012
Atlantic mackerel	—	—	—	—	—	0.813	—	—	—	—	—	—	1.000	0.813	0.062	0.875
Other pelagic	—	—	0.015	0.020	—	—	—	—	—	0.003	0.003	0.007	0.017	1.000	0.055	0.334
Other fish	0.005	—	—	0.012	—	—	—	—	—	—	0.002	0.025	—	0.407	1.000	0.447
Squids	—	—	—	0.020	—	—	—	—	—	0.002	0.008	0.001	0.023	0.215	0.071	1.000
POLAND																
Red hake	—	—	—	—	1.000	0.031	—	—	—	—	—	0.047	—	0.172	0.031	—
Pollock	—	—	—	—	—	1.000	—	—	—	—	—	—	—	—	0.250	—
Atlantic herring	0.004	—	—	—	—	—	—	—	—	—	0.012	1.000	0.258	0.034	0.039	0.024
Atlantic mackerel	0.003	—	—	0.001	—	—	—	—	—	—	0.012	0.075	1.000	0.006	0.056	0.027
Other pelagic	—	—	—	—	0.142	0.025	—	—	—	—	0.039	0.025	0.352	1.000	0.167	—
Other fish	—	—	—	0.092	0.167	—	—	—	—	—	0.017	0.033	0.317	0.125	1.000	—
Squids	—	—	—	0.034	—	—	—	—	—	—	0.057	0.080	0.231	0.144	0.197	1.000

APPENDIX TABLE 1.—Continued.

Species sought	Species caught															
	Atlantic cod	Haddock	Redfish	Silver hake	Red hake	Pollock	American plaice	Witch flounder	Yellowtail flounder	Other flounders	Other groundfish	Atlantic herring	Atlantic mackerel	Other pelagic	Other fish	Squids
ROMANIA																
Herring	—	0.007	0.007	0.020	—	—	—	—	0.016	—	—	1.000	0.223	0.035	—	—
Mackerel	—	—	—	0.008	—	—	—	—	—	—	0.064	0.051	1.000	0.058	0.010	0.026
SPAIN																
Atlantic cod	1.000	0.065	—	—	0.001	0.134	—	—	—	—	0.008	—	—	—	—	—
Squids	—	—	—	—	—	—	—	—	—	—	0.003	—	—	—	—	1.000
U.S.S.R.																
Silver hake	0.005	0.001	0.034	1.000	0.236	0.003	0.001	0.001	0.002	0.004	0.062	0.069	0.303	0.006	0.188	0.073
Red hake	0.020	—	0.019	0.410	1.000	0.009	0.003	0.004	0.007	0.011	0.117	0.118	0.237	0.002	0.107	0.032
Other groundfish	0.494	—	—	0.571	0.101	—	0.002	0.012	0.035	0.058	1.000	0.164	0.148	0.036	0.031	—
Atlantic herring	0.011	—	—	0.187	0.140	—	0.003	0.002	0.004	0.007	0.100	1.000	0.227	0.001	0.110	—
Atlantic mackerel	0.010	0.005	0.017	0.147	0.094	0.017	0.002	0.003	0.001	0.005	0.051	0.301	1.000	0.003	0.082	0.017
Other pelagic	—	—	—	0.092	0.299	—	—	—	—	—	—	—	0.055	1.000	0.061	0.001
Other fish	0.068	0.003	0.010	0.147	0.245	0.126	0.024	0.026	0.006	0.056	0.675	0.099	0.250	0.020	1.000	0.059
UNITED STATES																
Atlantic cod	1.000	0.075	0.013	0.002	—	0.052	0.009	0.004	0.035	0.088	0.056	—	—	—	0.001	—
Haddock	0.343	1.000	0.006	—	—	0.087	—	0.006	0.056	0.045	0.017	—	—	—	—	0.003
Redfish	0.039	0.006	1.000	0.001	—	0.066	0.005	0.007	—	—	0.046	—	—	—	—	0.001
Silver hake	0.054	0.003	0.010	1.000	0.022	0.010	0.007	0.006	0.004	0.016	0.058	0.014	0.002	0.008	0.009	0.025
Red hake	0.023	—	—	0.241	1.000	—	—	—	0.148	0.132	0.357	0.011	0.001	0.096	0.216	0.077
Pollock	0.168	0.054	0.045	0.028	0.008	1.000	0.007	0.021	0.007	0.004	0.130	0.001	—	—	0.001	0.005
Yellowtail flounder	0.091	0.014	0.001	0.001	—	0.001	0.010	0.020	1.000	0.053	0.004	—	—	0.001	—	0.003
Other flounder	0.492	0.074	0.003	0.013	0.003	0.014	0.125	0.230	0.423	1.000	0.072	—	—	0.003	0.005	0.002
Other groundfish	0.344	0.108	0.063	0.197	0.088	0.188	0.019	0.033	0.070	0.148	1.000	0.023	0.003	0.017	0.069	0.041
Atlantic herring	0.001	—	—	—	—	—	—	—	—	—	—	1.000	0.002	0.006	—	—
Atlantic mackerel	—	—	—	0.018	0.014	0.018	—	—	0.004	0.016	0.148	0.059	1.000	0.087	0.024	0.164
Other pelagic	0.003	—	—	0.125	0.003	—	—	—	0.003	0.006	0.030	—	0.064	1.000	0.107	0.189
Other fish	0.010	—	—	—	—	—	—	0.010	—	—	—	—	—	0.160	1.000	—
Squids	—	—	—	0.015	0.002	—	—	—	—	0.091	0.110	—	0.005	0.025	0.005	1.000

APPENDIX TABLE 2.—Linear programming simulation by country in ICNAF Subarea 5 and Statistical Area 6, 1975 catches to maximize total catch (1,000 t). Simulated using 1973 bycatch ratios. Actual directed and total catches are included also.

Species sought	Total allowable catch constraint	Simulated		Actual	
		Directed catch	Total catch	Directed catch	Total catch
BULGARIA					
Atlantic cod	0.07	—	0.03	—	—
Redfish	0.50	—	0.03	—	—
Silver hake	2.00	—	0.92	1.02	1.92
Red hake	5.41	—	0.23	—	0.03
Yellowtail flounder	0.14	—	0.06	—	<0.01
Other groundfish	0.65	—	0.13	—	0.34
Atlantic herring	1.20	0.47	1.20	—	0.42
Atlantic mackerel	18.75	18.64	18.75	18.47	18.75
Other pelagic	0.75	—	0.15	—	0.39
Other fish	2.60	—	0.48	—	2.63
Squids	1.70	—	0.24	—	0.21
Total	34.40		22.22		24.70
CANADA					
Atlantic cod	4.82	0.55	1.31	1.10	1.93
Haddock	1.20	—	0.60	0.44	1.44
Redfish	0.50	—	0.02	0.01	0.06
Pollock	2.46	—	2.46	4.13	4.74
American plaice	<0.01	—	<0.01	—	0.02
Witch flounder	<0.01	—	<0.01	—	0.01
Yellowtail flounder	0.02	—	<0.01	—	0.01
Other flounder	0.03	—	0.02	—	0.05
Other groundfish	0.78	0.70	0.76	0.30	0.66
Atlantic herring	9.00	9.00	9.00	5.08	5.08
Atlantic mackerel	7.50	—	0.06	—	<0.01
Other pelagic	0.01	0.01	0.01	—	—
Total	26.32		14.24		14.00
FRANCE					
Other groundfish	0.02	—	0.02	—	—
Atlantic herring	1.87	1.87	1.87	3.34	3.34
Squids	3.40	0.87	0.87	—	—
Total	5.29		2.76		3.34
FEDERAL REPUBLIC OF GERMANY					
Atlantic cod	0.09	—	0.01	—	0.02
Silver hake	0.50	—	0.04	—	0.04
Pollock	1.60	1.60	1.60	0.10	0.15
Other groundfish	0.90	0.48	0.90	—	0.02
Atlantic herring	24.50	24.50	24.50	22.99	23.01
Atlantic mackerel	1.40	0.99	1.40	0.08	0.47
Other pelagic	0.51	—	0.35	—	1.46
Other fish	0.39	—	0.25	—	—
Squids	1.00	0.68	1.00	—	0.03
Total	30.89		30.05		25.20
GERMAN DEMOCRATIC REPUBLIC					
Atlantic cod	1.30	—	0.03	—	0.03
Redfish	0.63	—	0.02	—	0.01
Silver hake	3.10	—	0.06	—	0.04
Pollock	3.50	3.49	3.50	<0.01	0.10
Other groundfish	<0.01	—	—	—	0.07
Atlantic herring	31.90	13.00	13.75	27.00	30.90
Atlantic mackerel	56.25	20.00	20.14	47.95	48.34
Other pelagic	0.06	—	0.06	—	0.06
Other fish	2.94	—	2.90	0.12	2.18
Squids	1.30	—	0.06	—	0.90
Total	100.98		40.52		82.63
JAPAN					
Atlantic cod	0.05	—	—	—	—
Redfish	0.50	—	0.12	—	0.02
Silver hake	7.30	—	0.35	—	<0.01
Red hake	0.03	—	—	—	<0.01
Pollock	0.25	—	0.25	—	—
Other flounder	0.06	—	0.04	—	—
Other groundfish	0.10	—	0.10	0.33	1.13
Atlantic herring	1.16	1.09	1.16	1.88	1.88
Atlantic mackerel	0.80	0.31	0.65	0.08	0.20
Other pelagic	9.30	6.71	9.30	2.65	3.62
Other fish	1.50	0.37	1.50	—	—
Squids	24.30	9.89	12.58	13.25	13.99
Total	45.35		26.05		20.84
POLAND					
Atlantic cod	0.49	—	0.37	—	0.48
Redfish	0.40	—	—	—	<0.01
Silver hake	5.30	—	0.13	0.24	0.38
Red hake	2.20	2.12	2.20	—	—
Pollock	0.35	0.28	0.35	—	0.02
Other groundfish	1.40	—	1.40	—	1.11
Atlantic herring	38.40	32.14	38.40	33.05	38.46
Atlantic mackerel	90.00	81.45	90.00	68.45	74.28
Other pelagic	2.20	0.15	2.20	0.17	3.77
Other fish	6.40	0.34	6.40	—	1.71
Squids	6.80	0.45	3.42	3.25	6.84
Total	153.94		144.87		127.05
ROMANIA					
Haddock	0.01	—	<0.01	—	—
Redfish	0.34	—	<0.01	—	0.01
Silver hake	0.50	—	<0.01	—	0.12
Yellowtail flounder	0.01	—	<0.01	—	—
Other groundfish	0.15	—	0.01	—	<0.01
Atlantic herring	0.20	0.20	0.20	1.54	1.54
Atlantic mackerel	3.75	0.05	0.10	—	0.07
Other pelagic	0.13	—	0.13	—	—
Other fish	0.02	—	0.02	—	—
Squids	0.60	—	<0.01	—	0.05
Total	5.71		0.46		1.79
SPAIN					
Atlantic cod	7.09	1.49	1.49	4.07	4.07
Haddock	0.30	—	0.10	—	0.07
Red hake	0.07	—	<0.01	—	0.01
Pollock	0.42	—	0.42	—	0.10
Other groundfish	0.10	—	0.05	—	0.42
Squids	13.00	13.00	13.00	9.90	9.90
Total	20.98		15.06		14.57
U.S.S.R.					
Atlantic cod	2.50	—	0.24	—	2.43
Haddock	0.05	—	0.05	—	0.01
Redfish	1.44	—	1.44	—	1.37
Silver hake	113.30	40.20	41.22	71.38	88.88
Red hake	44.40	—	11.18	4.50	26.12
Pollock	1.26	—	0.20	—	0.19
American plaice	0.20	—	0.05	—	0.18
Witch flounder	0.20	—	0.05	—	0.20
Yellowtail flounder	0.84	—	—	—	0.08
Other flounder	0.60	—	0.20	—	0.56
Other groundfish	16.70	—	2.79	—	2.86
Atlantic herring	42.10	1.91	5.28	37.08	40.95
Atlantic mackerel	101.25	1.96	14.80	99.91	106.31
Other pelagic	4.40	4.15	4.40	—	0.68
Other fish	28.90	—	8.20	5.99	34.08
Squids	8.50	—	3.00	3.53	8.94
Total	366.64		93.10		313.84
UNITED STATES					
Atlantic cod	28.00	14.35	28.00	12.46	23.41
Haddock	4.50	—	4.50	0.86	5.09
Redfish	20.62	18.24	20.62	7.07	8.96
Silver hake	43.00	34.49	43.00	17.79	20.59
Red hake	12.90	9.71	12.90	0.11	2.43
Pollock	11.50	4.19	11.50	3.80	8.06
American plaice	2.50	—	1.10	0.26	2.19
Witch flounder	4.10	—	1.65	0.36	2.03
Yellowtail flounder	15.00	11.02	15.00	14.99	19.32
Other flounder	17.30	—	6.28	11.81	19.39
Other groundfish	44.88	26.20	34.80	10.34	19.11
Atlantic herring	24.65	23.20	24.65	35.76	36.09
Atlantic mackerel	4.70	4.11	4.70	0.54	1.65
Other pelagic	9.52	5.95	9.52	19.61	23.40
Other fish	13.60	8.62	13.60	17.02	27.65
Squids	5.60	1.04	5.60	0.21	1.67
Total	262.37		237.42		221.04

APPENDIX TABLE 3.—Linear programming simulation by country in ICNAF Subarea 5 and Statistical Area 6 of catches to maximize total catch (1,000 t). Simulated using 1971 bycatch ratios. Actual directed and total catches are included also.

Species sought	Total allowable catch constraint	Simulated		Actual	
		Directed catch	Total catch	Directed catch	Total catch
BULGARIA					
Atlantic cod	0.70	—	0.01	—	—
Haddock	0.01	—	0.01	—	—
Redfish	0.50	—	—	—	—
Silver hake	2.00	0.88	1.82	1.02	1.92
Flounders	0.14	—	0.14	—	<0.01
Other groundfish	6.06	0.78	1.76	—	0.37
Atlantic herring	1.20	—	1.20	—	0.42
Other pelagic	19.50	18.39	19.50	18.47	19.15
Other fish + squids	4.30	—	4.30	—	2.84
Total	34.41		28.74		24.70
CANADA					
Atlantic cod	4.82	—	0.75	1.10	1.93
Haddock	1.20	—	0.37	0.44	1.44
Redfish	0.50	—	0.05	0.01	0.06
Flounders	0.05	—	0.05	—	0.09
Other groundfish	3.24	2.78	2.78	4.43	5.40
Atlantic herring	9.00	9.00	9.00	5.08	5.08
Other pelagic	7.51	7.51	7.51	—	<0.01
Total	26.32		20.51		14.00
FEDERAL REPUBLIC OF GERMANY					
Atlantic cod	0.09	—	—	—	0.02
Silver hake	0.50	—	—	—	0.04
Other groundfish	2.50	—	0.27	0.10	0.17
Atlantic herring	24.50	24.50	24.50	22.99	23.01
Other pelagic	1.91	—	0.54	0.08	1.93
Other fish + squids	1.39	—	—	—	0.03
Total	30.89		25.31		25.20
GERMAN DEMOCRATIC REPUBLIC					
Atlantic cod	1.30	—	—	—	0.03
Redfish	0.63	—	—	—	0.01
Silver hake	3.10	—	—	—	0.04
Other groundfish	3.50	0.54	3.50	<0.01	0.17
Atlantic herring	31.90	30.63	31.90	27.00	30.90
Other pelagic	56.31	20.23	24.53	47.95	48.40
Other fish + squid	4.24	—	4.24	0.12	3.08
Total	100.98		64.17		82.63
JAPAN					
Atlantic cod	0.05	—	0.01	—	—
Redfish	0.50	—	0.01	0.12	0.02
Silver hake	7.30	—	0.03	0.35	0.01
Flounders	0.06	—	0.01	0.04	—
Other groundfish	0.38	—	0.38	0.35	1.13
Atlantic herring	1.16	1.15	1.16	1.88	1.88
Other pelagic	10.10	4.49	4.50	2.73	3.82
Other fish + squids	25.80	—	1.51	13.24	13.99
Total	45.35		7.59		20.84
POLAND					
Atlantic cod	0.49	—	0.14	—	0.48
Redfish	0.40	—	0.09	—	<0.01
Silver hake	5.30	—	0.09	0.24	0.38
Other groundfish	3.95	—	0.25	—	1.13
Atlantic herring	38.40	26.01	38.40	33.05	38.46
Other pelagic	92.20	85.90	92.20	68.62	78.05
Other fish + squids	13.20	1.48	13.20	3.25	8.55
Total	153.94		144.37		127.05
ROMANIA					
Haddock	0.01	—	<0.01	—	—
Redfish	0.34	—	—	—	0.01
Silver hake	0.50	—	0.01	—	0.12
Flounders	0.01	—	0.01	—	—
Other groundfish	0.15	—	<0.01	—	<0.01
Atlantic herring	0.20	—	0.04	1.54	1.54
Other pelagic	3.88	0.14	0.15	—	0.07
Other fish + squids	0.62	—	0.06	—	0.05
Total	5.71		0.27		1.79
SPAIN					
Atlantic cod	7.09	1.71	1.71	4.07	4.07
Haddock	0.30	—	0.30	—	0.07
Redfish	0.07	—	—	—	—
Other groundfish	0.52	—	0.09	—	0.53
Other fish + squids	13.00	13.00	13.00	9.90	9.90
Total	20.98		15.10		14.57
U.S.S.R.					
Atlantic cod	2.50	—	0.38	—	2.43
Haddock	0.05	—	0.05	—	0.01
Redfish	1.44	—	1.44	—	1.37
Silver hake	113.30	10.00	17.73	71.38	88.88
Flounders	1.84	—	1.84	—	1.02
Other groundfish	62.36	0.14	6.14	4.50	29.17
Atlantic herring	42.10	34.46	42.10	37.08	40.95
Other pelagic	105.65	39.85	47.33	99.91	106.99
Other fish + squids	37.40	—	10.01	9.52	43.02
Total	366.64		127.02		313.84
UNITED STATES					
Atlantic cod	28.00	—	15.54	12.46	23.41
Haddock	4.50	—	4.50	0.86	5.09
Redfish	20.62	16.59	20.62	7.07	8.96
Silver hake	43.00	32.77	43.00	17.79	20.59
Flounder	38.90	1.32	34.20	27.42	42.93
Other groundfish	69.28	59.84	69.28	14.25	29.60
Atlantic herring	24.65	10.65	24.65	35.76	36.09
Other pelagic	14.22	12.56	14.22	20.15	25.05
Other fish + squids	19.20	9.86	19.20	17.23	29.32
Total	262.37		245.21		221.04

NOTES

EFFECT OF SWIMMING SPEED ON THE EXCESS TEMPERATURES AND ACTIVITIES OF HEART AND RED AND WHITE MUSCLES IN THE MACKEREL, *SCOMBER JAPONICUS*

Body temperatures of most fish typically are about the same as the water in which they swim for much of the heat generated by muscular activity is ducted away via the circulating blood and lost by convection at the gills and body surface.

Some scombrids and lamnid sharks conserve muscle heat using countercurrent vascular heat exchangers (retia mirabilia) so that temperatures are maintained significantly above ambient in the brain, eyes, red and white swimming muscles, and viscera (Carey et al. 1971; Stevens and Fry 1971; Linthicum and Carey 1972; Graham 1973). In other fishes lacking these heat conserving devices, only small temperature excesses above ambient have been recorded, but rarely more than 1°C (Stevens and Fry 1974). Since heat production must depend primarily on work output by the locomotor musculature, we have examined effects of swimming speed on the magnitude of the small temperature excesses in a "cool" scombrid not equipped with the retia exchangers, the mackerel, *Scomber japonicus* (locally the Pacific mackerel = chub mackerel).

Another important question concerning scombrid locomotion is how contractions of red and white muscle fibers are staged as swimming speed increases. It is generally thought that red muscle provides power for cruise swimming and that white muscle functions in "burst" swimming (Rayner and Keenan 1967). Red muscle is predominately aerobic and utilizes fatty acids as the major energy source whereas white muscle (which uses glycogen) usually functions anerobically (Gordon 1968; Bilinski 1974). The second objective of our study was to determine how heart rate and red and white muscle activity of *S. japonicus* are affected by swimming speed. For this purpose, electrodes were implanted into the pericardial space and in swimming muscles of fish so that simultaneous records of electrocardiograms (ECG's) and red and white electromyographs (EMG's) could be obtained.

The genus *Scomber* is a primitive member of the family Scombridae (Kishinouye 1923). It has a fusiform shape, is less heavily bodied than the skipjack tuna, *Katsuwonus pelamis*, and other tunas, but shares several characteristics with warm-bodied species; they swim continuously (swim bladders are reduced or absent), have high rates of oxygen consumption (Baldwin 1923; Hall 1930), and have high blood hemoglobin levels (Greer-Walker and Pull 1975). They are also obligatorily dependent upon ram gill ventilation as adults (Roberts 1975) and have large gill surface areas with a high diffusion efficiency (Hughes 1966; Steen and Berg 1966).

Materials and Methods

Surgical Procedures and Swimming Experiments

The general procedure was to implant either thermocouples or cardiac (ECG) and muscle (EMG) electrodes into mackerel which were then placed in a Blažka-Fry tunnel respirometer (12 cm i.d.) to swim at controlled velocities. Fifteen specimens (35-40 cm fork length (FL); 0.38-0.62 kg) were obtained from regularly replenished and maintained mackerel stocks at the Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA. After netting, each fish was anesthetized in a large basin of oxygenated seawater containing 0.2 g/l of tricaine methanesulfonate (Crescent Research Chemical, Inc.)[1] and placed on an operating table where its gills were perfused continuously with a fast flow of oxygenated seawater containing a small amount of the same anesthetic (0.08 g/l). Thermocouples (0.127 mm in diameter copper constantan, polyvinyl chloride insulation) or electrode pairs (hooked, 0.07 mm in diameter stainless-steel, epoxy insulated) were implanted within the pericardial cavity just posterior to the ventricle, and in red and white muscles just under the leading edge of the second dorsal fin.

The white muscle thermocouple tip was placed midway between the vertebral column and the lateral edge of the body at the level of the horizontal midline. Preliminary dissections confirmed that red muscle in *S. japonicus* occurs in bands

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

that are concentrated below the skin along the lateral midline and become thicker posteriorly (see also Kishinouye 1923, fig. 16; Braekkan 1959, fig. 1). To ensure that the tip of the red muscle thermocouple would remain in place, the wire was passed from near the second dorsal fin obliquely through white muscle and then into the thin red muscle band. Once inserted, its position was easily verified by gentle fingertip probing.

To facilitate positioning of the two muscle thermocouples, 3-4 cm deep holes were tapped with a 20-gage hypodermic needle. The heart thermocouple was passed into the pericardial cavity through a 17-gage needle that was subsequently withdrawn. All wires were anchored in place by skin sutures. Wire leads (1 m long) to the recorder were lap wound together, passed posteriorly, and sutured to the dorsal midline near the finlets to prevent tangling around the tail. Implanting required about 15 min after which the fish was transferred to the respirometer swimming tube where aerated water was circulated over the gills by the driving impeller at a slow speed.

Two hours recovery from anesthesia and a brief period of swim training was required before a fish could maintain station in the tube and regulate swimming speed in response to water flow. This time delay also allowed stabilization of tissue temperature at ambient conditions following surgery.

Adaptation to the swimming chamber was carried out at a basal swimming speed which is 1.5 BL/s (body lengths per second) for *S. japonicus* (Magnuson 1973). This speed is also just above the velocity required for sustained ram gill ventilation (Roberts 1975). Flow rates in the respirometer were calibrated with a ducted flowmeter (Marine Advisors, Inc. model B-7C) and controlled by altering the applied armature voltage to the impeller pump motor. Eight fish were used for excess temperature measurements and seven were used to monitor EMG (4) and ECG (3) patterns.

Calibration Procedures

Thermocouples were made by soldering together the twisted bared tips of the copper and constantan wires and sealing them with epoxy cement. The three tissue thermocouples and a reference thermocouple (for respirometer water temperature) were each connected in series (constantan leads) to an ice-bath reference couple (0°C) and to an RS Beckman Dynograph (copper leads) through a high-quality, shorting rotary-switch. This arrangement permitted rapid switching between thermocouples without opening the recorder circuit. Thermocouples were standardized in a water bath at 20°±0.05°C before and after each trial.

Paired electrodes for recording ECG's and EMG's were prepared and implanted (in the same sites used for thermocouples) as described by Roberts (1975). The ECG and EMG signals were preamplified using high impedence, probe amplifiers (Grass, P511DR) to improve the frequency response of the RS Dynograph.

Seawater was kept continuously flowing through the respirometer tube and ambient temperature was maintained within 2.0°C in each experiment by mixing warm and cold seawater at the outlet taps of the laboratory seawater system. Over the 2-mo course of experiments, respirometer temperatures ranged from 16° to 22°C.

Results

Changes in excess tissue temperatures that accompany increased swimming speed in the mackerel are best seen in a particularly successful trial with fish number 6 (Figure 1). Similar, but somewhat variable records of heart, and red and white muscle temperatures were obtained for all fish (Table 1).

While cruising at low speeds, excess temperatures reached a maximum of about 0.3°C in the red and white muscles, but doubled within 3 min swimming at enforced higher speeds (3.2-4.5 BL/s). Excess temperatures recorded in the heart averaged about one-half of the excess developed in muscles at all swimming velocities. When swimming speeds were reduced once again to slow cruising, excess temperatures returned to pre-burst levels within 8-15 min.

During bouts of prolonged high-speed swimming (5-6 min), water in the swimming tunnel was warmed about 1°C due to frictional heating even though a continuous exchange of seawater was maintained from the supply tap (about 15 l/min). This thermal error was minimized by rapidly accelerating the fish from slow cruising to its predetermined, burst-swimming velocity. In Figure 1 for example, the fish was accelerated from 1.4 to 3.9 BL/s in about 5 s followed by sustained swimming for 3 min, and then rapidly decelerated to 1.4 BL/s. Equilibration of tissue thermal excess (i.e., generation minus dissipation) occurred in most

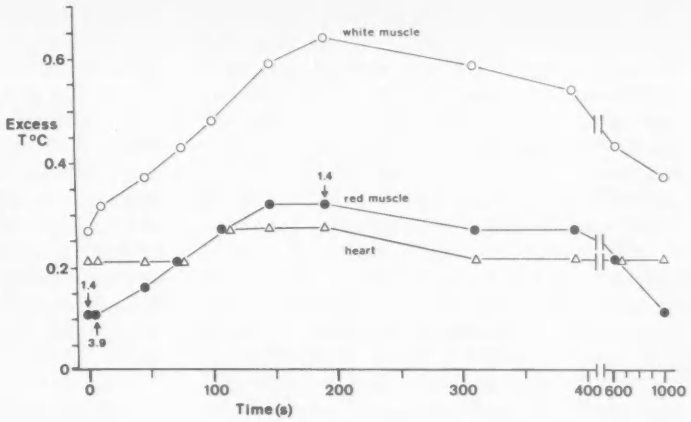

FIGURE 1.—Temperature excess in the heart and in red and white muscles recorded from *Scomber japonicus* no. 6 (35 cm FL, 0.45 kg) swimming at speeds from 1.4 to 3.9 BL/s. Arrows indicate timing and direction of speed changes. Ambient temperature, 19.5°-19.6°C.

TABLE 1.—Temperature excesses as ΔT (°C) recorded for seven *Scomber japonicus* swimming at basal and moderately fast speeds in body lengths per second (BL/s).[1]

Item	Fish number 1	2	3	4	6	7	8	Mean
Fork length (cm)	35.6	39.2	38.9	38.1	35.0	36.3	34.3	36.8
Weight (kg)	0.54	0.62	0.59	0.55	0.45	0.58	0.39	0.53
Highest ΔT at basal speed (1.3-1.9 BL/s) in:								
Red muscle	0.2	0.1	0.2	0.2	0.2	0.3	0.5	0.24
White muscle	0.2	0.3	0.3	0.2	0.4	0.3	0.3	0.29
Heart	0.0	0.3	0.1	0.1	0.2	0.2	[2]	0.15
Highest ΔT and swimming speeds (BL/s) in:								
Red muscle	0.9 (4.2)	0.75 (3.2)	0.55 (3.7)	0.85 (4.2)	0.3 (3.9)	0.5 (3.8)	0.8 (4.3)	0.66 (3.9)
White muscle	0.75 (4.2)	0.8 (3.2)	0.65 (3.7)	0.6 (3.9)	0.65 (3.9)	0.3 (3.8)	0.7 (4.3)	0.64 (3.9)
Heart	0.45 (4.2)	[2]	[2]	0.4 (4.5)	0.25 (3.9)	0.25 (3.8)	[2]	0.34 (4.1)
Maximum trial speed (BL/s)	4.2	3.2	3.7	4.5	3.9	3.8	4.3	3.9
Water temperature, range (°C)[3]	16.1-17.0	16.5-17.0	16.8-17.8	17.1-17.5	19.5-19.6	20.5-21.0	21.1-21.8	

[1]Fish no. 5 omitted because it would not swim in the respirometer tube.
[2]Thermocouple malfunction.
[3]Starting temperature is that of the seawater supply from mid-June to mid-July.

cases within the 3-min swimming bouts. Although the thermal excess was greater in white muscle of fish number 6 (Figure 1), mean maximum temperature excesses recorded in red and white muscles of the seven mackerel were about the same (Table 1).

Variability observed in excess temperature measurements seems attributable to different performances of individual fish. Some specimens had more body fat than others and did not swim steadily. Others were affected by the trailing thermocouple cable as evidenced by their tail-beat patterns. The cable also added drag which reduced speed but probably increased total heat production at a specific speed. None of the fish trailing thermocouple cables could swim steadily above 5 BL/s, whereas fish trailing the thinner ECG and EMG cables could maintain a speed of 6 BL/s. Some of the variability in recorded thermal excesses may have also been due to the slightly differing locations of thermocouples in each fish. In addition, trauma due to thermocouple insertion, which probably interrupts normal blood flow locally may have been a factor influencing thermal convection. In a few cases, thermocouple signals changed abruptly possibly because of insulation failure at the tip due to rapid body flexing of fishes at higher swimming speeds.

A wide range was found in heart rates of mackerel cruising at 1-1.5 BL/s (mean, 106; range, 80-140 beats/min). With acceleration to 4-5 BL/s, the mean heart rate increased by 54% (mean, 130; range, 112-150), but rapidly returned to the resting rate within a few minutes of deceleration.

The EMG's demonstrate that both red and white muscle fibers contract synchronously while the mackerel swims at 2 BL/s (Figure 2). At slower velocities, even below basal speed, both red and white fibers were active during each tail-beat cycle. With acceleration to velocities above cruising, rates and amplitudes of both red and white EMG's showed proportionate increases; red muscle EMG'S reached maximal amplitude between 3 and 4 BL/s. White muscle EMG's of the first mackerel tested appeared to increase in amplitude more than red muscle, and in proportion to velocity up to the highest speed at which the fish could swim steadily (about 6 BL/s). However, subsequent records obtained from three other fish did not confirm a consistent pattern of amplitude development with swimming velocity in the two fiber types. Variations in EMG amplitudes of single tail-beat cycles were commonly found in the recordings of all the fish from both red and white muscles at all swimming speeds. This is evident in the 1-s records for the fish in Figure 2. In this case, amplitude variability was more apparent at 5.9 BL/s because the fish's swimming became erratic—characterized by asymmetrical tail beats (unsteady or dart swimming). High-speed bilateral recording as used by Hudson (1973) would have aided the analysis. Figure 2 also shows that large bursts in white muscle sometimes accompany small bursts in red muscle, but confirmation of interactive contractile events in red and white muscles was not attempted.

Discussion

Body Temperatures

This study shows that *Scomber japonicus*, a strong continuous swimmer, does not develop large temperature excesses in its tissues while swimming at basal (1.3-1.9 BL/s) or sustainable (3-5 BL/s) speeds. Temperature excesses measured in the heart and in red and white muscles of this fish never exceeded 1°C and thus are not different from values typically found in species without specialized heat-conserving retia mirabilia (Lindsay 1968; Carey et al. 1971; Stevens and Fry 1974).

At high speeds, the lowest thermal excesses measured for the mackerel were in the heart. It was not possible to discriminate between heat actually produced by increased cardiac activity and that transported to the heart either via the blood (i.e., convectively) or by conduction. Some heat production must occur in the heart, but its mass is small compared with the volume of blood pumped per unit of time. Thus much of the muscle heat is either dissipated at the body surface or is conducted very slowly to other tissues before it reaches the heart and gills. There are several reasons why muscle heat may not reach the heart in venous blood. First, blood warmed in active muscles would be cooled as it mixes with blood returning from metabolically less active tissues. Also some countercurrent heat transfer (i.e., from

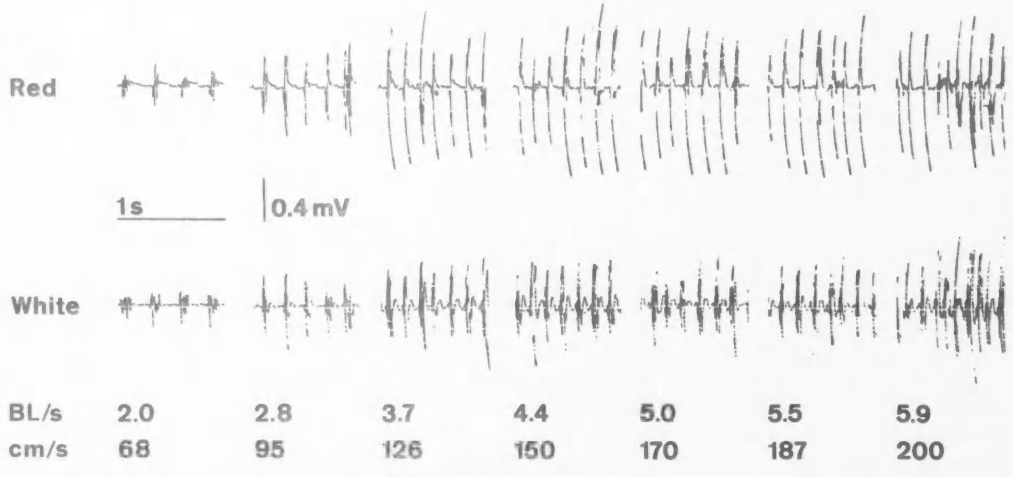

FIGURE 2.—Red and white electromyographs of a *Scomber japonicus* (34 cm FL, 0.39 kg) accelerating from 2.0 to 5.9 BL/s (68-200 cm/s) as indicated below EMG traces. Ambient temperature, 17°C.

a warm vein to an artery) between parallel and closely positioned arteries and veins (either segmental vessels or postcardinal vein and dorsal aorta) could reduce convective heat transport. For example, Stevens and Sutterlin (1976) demonstrated a mechanism of this type that transferred heat directly from afferent to efferent gill arteries in the sea raven, *Hemitripterus americanus*.

Fish body temperatures are not uniform. In most species, including the warm-bodied forms, the highest thermal excesses occur in deep muscles (both red and white) where body thickness is maximum (Lindsey 1968; Carey et al. 1971; Graham 1975). For this reason white muscle temperatures in the mackerel might be higher in more anterior regions of the body (i.e., at the first dorsal fin) where the white muscle mass and body thickness are greater. By contrast, higher temperatures in red muscle would not be expected because in *Scomber* this tissue is a thin band along the side of the body, only reaching maximum thickness as the body tapers toward the caudal peduncle (see figures in Kishinouye 1923 and Braekkan 1959).

Red and White Muscle Activity at Different Swimming Speeds

We were unable to determine a specific velocity where white muscle is recruited for swimming in the mackerel. At very low speeds, tail beats often became erratic or excessively strong. This may have been due to the added cable drag. Also, the basal speeds for fish in this study coincide with their minimum velocity needs for ram gill ventilation (Roberts 1975) which may have elicited struggling at slow speeds. Our EMG's do show low amplitude, synchronous potentials in both red and white muscles that were correlated with tail beats from very slow speeds up to about 2 BL/s. Amplitudes of EMG's in both muscle types seemed to reach a maximum for steady swimming at 3-4 BL/s, demonstrating that white fibers are active well within the range of sustainable cruising velocities for this species and that red muscle remains active at high speeds.

Neither patterns of motor innervation of red and white muscle fibers (focal or distributed) of scombrid myotomes nor the nature of their electrical responses seem to be known. Whether the compound potentials we recorded represent all-or-none spikes, abortive spikes, or rapid drifts in membrane potentials (local potentials) following excitation, also is unknown.

We suggest that the amplitude changes recorded from both the red and white fibers as the fish accelerated represent fiber recruitment. White muscle electrodes were located close to the vertebral column, probably not closer than 1 cm to the lateral strips of red muscle, so detection of conducted red fiber potentials was unlikely. Amplitude variations detected in both muscle types during single tail-beat cycles was considerable. These variations were attributed to movement artifacts and possible drop-out of motor units nearby the electrodes.

A nearly completed dissertation study in one of our laboratories has demonstrated clearly that EMG's of red muscle in striped bass, *Morone saxatilis*, and in bluefish, *Pomatomus saltatrix*, also grade in amplitude with increasing swimming speed up to about 3 BL/s (M. A. Freadman, Graduate Student, Department of Zoology, University of Massachusetts, Amherst, MA 01003. Pers. commun., September 1977). But unlike *S. japonicus*, white muscle activity in these species does not appear until they reach burst-swimming velocities—a pattern of red and white muscle activation that resembles the herring (Bone 1975).

Red and white muscle fibers have different anatomical, physiological, and biochemical characteristics that relate directly to their roles in the swimming of different fishes (George 1962; Bone 1966; Bilinksi 1974; Johnston et al. 1977). In some species red muscle functions over a wide range of speeds whereas white muscle is used only in burst swimming (Bone 1966). Staging in the activity of red and white muscles, that is the recruitment of white (mosaic red and white mixed as in salmonids; pink and white as in some carp) as velocity increases, has been observed in many species (viz., dogfish, Bone 1966; skipjack tuna, Rayner and Keenan 1967; rainbow trout, Webb 1971, Hudson 1973; coalfish, Greer Walker 1971; and carp, Johnston et al. 1977). The relative contribution of these muscle types to swimming no doubt relates to species-specific locomotory requirements for cruise swimming and maneuverability. However, more recently acquired data on this point show, as in *S. japonicus*, that white muscle fibers do often function at low, sustainable swimming speeds (e.g., in coalfish and carp) and thus are not exclusively reserved for high-speed burst swimming (Johnston et al. 1977).

For scombrids, which swim continuously and rely upon forward motion to ventilate their gills, the existence of a relatively high speed for the division of labor between red and white muscles, has been assumed primarily on the basis of work done by Rayner and Keenan (1967). These investigators concluded that in the skipjack tuna, red muscle alone powered cruise swimming and white muscle only became active at burst velocities. The initial objective of Rayner and Keenan's study was to demonstrate contractile properties of red muscle, and to this end they blocked white muscle activity (pentobarbital) and worked exclusively with tranquilized (proprioprom azine) or sedated fish. Moreover, their specimens were restrained in a fixed position and artificially ventilated by perfusion tubes in the mouth. Thus the movements by these skipjack tunas that were identified as "low frequency swimming," were in fact only casually related to the swimming requirements for gill ventilation and hydrostatic equilibrium; both are controlling factors in normal swimming (Magnuson 1973; Roberts 1975).

Our results with *S. japonicus* contrast in that they show both red and white muscles function in low-speed swimming. Also, Dizon and Brill (A. E. Dizon, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812. Pers. commun., September 1977) recorded red and white EMG's from yellowfin tuna, *Thunnus albacares*, and found that white muscle activity begins at swimming velocities of <3 BL/s—a speed only slightly above the minimum for hydrostatic equilibrium and well below maximal burst capabilities (Magnuson 1973). These observations indicate that in fast-swimming scombrids, patterned staging of red and white muscle activity may differ in that activity begins in white fibers at very low speeds, and that both red and white muscle remain active throughout a wide range of sustainable speeds as well as at burst velocities. Implicit in this idea is the presence of a high scope for aerobic activity in scombrid white muscle which has been recently demonstrated for the skipjack tuna (Guppy et al. in press). Also required by the hypothesis are specializations in red muscle for high-speed contraction which is supported by the findings of Johnston and Tota (1974) that high levels of myofibrillar ATPase occur in the red muscle of bluefin tuna, *T. thynnus*.

What physiological advantage might be gained by a 1°C thermal excess during fast swimming? Assuming a Q_{10} of 2 then a 10% increase in metabolism would afford about a 2-3% rise in swimming speed, but an insignificant change in overall swimming efficiency (Webb 1971). An interesting speculation is that the extensive heat-exchanging vascular network used for endothermy in the scombrids may have initially evolved to meet the high oxygen requirements of red and white myotomal muscle. More metabolic heat is produced during aerobic respiration and natural selection may have proceeded toward a vascular design that maximized oxygen delivery, yet augmented muscle function by conserving heat and insulating the swimming musculature from ambient conditions.

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THERMAL BEHAVIORAL RESPONSES OF THE SPECKLED SANDDAB, *CITHARICHTHYS STIGMAEUS*: LABORATORY AND FIELD INVESTIGATIONS

The speckled sanddab, *Citharichthys stigmaeus*, is a small bothid flatfish that is common in southern California (Ford 1965; Stephens et al. 1974). These authors and Helly[1] have suggested that temperature may have a significant effect on localized population abundances and distributions of speckled sanddabs. No studies to date, however, have examined in detail the relationship between temperature and fish behavior and distribution.

We designed this work to study the speckled sanddab population in King Harbor, Redondo Beach, Calif. This harbor (Figure 1), which receives the thermal effluent from an electricity generating station as well as cold upwelled water from the adjacent Redondo Submarine Canyon, contains a highly diversified thermal environment (Stephens 1972).

[1]Helly, J. J., Jr. 1974. The effects of temperature and temperature selection on the seasonality of the bothid flatfish, *Citharichthys stigmaeus*. Honors Thesis, Occidental Coll., Los Ang., 34 p.

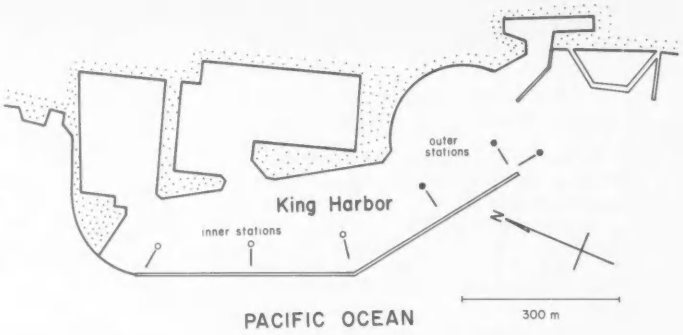

FIGURE 1.—Location of field sampling stations for speckled sanddabs in King Harbor, Redondo Beach, Calif.

Methods

We collected adult speckled sanddabs between August 1975 and January 1976 with a 3-m otter trawl. The fish were transported to the laboratory in aerated seawater and acclimated to a range of normally occurring temperatures (10.0°-19.7°C) according to the methods of Ehrlich et al. (1979). Prior to acclimating the speckled sanddabs, we removed the gill isopod *Livonica vulgaris* individually with forceps. During holding and acclimation, we fed the fish to satiation daily with live and frozen *Artemia salina*. The behavioral responses of the fish to temperature were studied using a 3.6-m long horizontal gradient and employing the techniques of Ehrlich et al. (1978). Each experiment lasted for 7-8 h with observations every 15 min. We shifted isotherm positions during each experiment to separate selection of temperature from preference for a given position within the experimental chamber.

Speckled sanddab abundance and distribution were studied using timed diver transects at six stations (Figure 1). Two divers swimming side by side for 5 min traversed each 6-m wide transect. They recorded the species and number of individuals observed in the same area. The transects by each pair of divers were run in duplicate on a monthly basis at each station from September 1974 through February 1976 and quarterly thereafter. In the analyses, we used the largest number of individual fish counted by either diver, but the average count of the two independent observations was used for estimates of large groups of fishes. The divers recorded the temperature at least twice during each transect, with thermometers readable to 0.5°C.

Results and Discussion

We examined the effects of acclimation temperature, size, and sex of speckled sanddabs on their temperature selection during 11 experiments (Table 1). The presence of some skewed temperature-specific frequency distributions (Table 1) precluded comparison of the results with parametric statistics. We tested these distributions for homogeneity using a Kruskal-Wallis test (Steel and Tor-

TABLE 1.—Temperatures selected by speckled sanddabs in laboratory experiments.

Date	No. test animals	No. fish observations	Standard length (mm) Mean	SD	Sex	Acclimation temperature (°C)	Selected temperature (°C) Mean	SD	Mode	Coefficient of skewness (g_1)	Coefficient of kurtosis (g_2)
21 Aug. 1975	9	265	96.3	0.6	not noted	14.0	10.5	3.4	10	0.493*	2.788
15 Dec.	8	230	91.5	1.3	not noted	10.0	12.3	4.5	9	0.543*	2.824
18 Dec.	8	218	88.5	3.2	M	19.7	10.5	4.1	8	0.673*	2.928
22 Dec.	9	220	90.3	3.5	F	18.9	10.1	2.6	9-10	0.427	3.438
5 Jan. 1976	9	210	77.1	4.0	M	15.2	10.9	2.6	11	0.220	3.512
8 Jan.	9	251	82.0	6.7	F	15.2	10.4	3.2	8-9	0.465	3.036
9 Jan.	9	250	82.0	6.7	F	15.2	11.6	3.6	8	0.573*	2.673
26 Jan.	6	162	76.3	5.6	M	12.0	9.9	4.3	8	0.400	0.592*
27 Jan.	6	167	71.5	2.7	M	12.0	10.5	2.5	9-10	0.291	2.372
29 Jan.	6	157	73.2	2.6	M	12.0	11.1	3.0	9	0.724*	2.538
30 Jan.	6	160	75.5	5.1	M	12.0	9.8	2.5	8	0.422	2.078

*$P<0.05$.

rie 1960) and detected no significant differences ($\chi^2_{10\,df} = 15.99$, $P > 0.05$). The overall mean selected temperature from pooled data was 10.8°C (SD = 3.1°C), and the mode was 9°C; 70% of all occurrences were in the range of 8°-13°C (Figure 2). The frequency distribution, however, was significantly skewed towards warmer temperatures (Figure 2).

Brett (1971) showed that the preferred temperature coincided with the optimal temperature for growth of sockeye salmon, *Oncorhynchus nerka*. Crawshaw (1977) found that physiological responses are often optimized in a zone of efficient operation rather than at a peak, and temperature preference reflects this. We are not aware of any work on the effects of temperature on the physiology of speckled sanddabs.

Considering the work of Brett (1971) and Crawshaw (1977), it is not unreasonable to suspect that speckled sanddabs may have a range of temperatures (approximately 8°-13°C) for efficient growth. The skewness may partially be due to activity increasing with temperature that could have resulted in occasional excursions into a greater number of compartments (temperatures) than at colder temperatures. Ehrlich et al. (1978) also suggested that skewness of a temperature-specific frequency distribution could result from preferred temperatures approaching lethal limits. These limits are not known for speckled sanddabs. DeWitt (1967) suggested that skewness of distribution could result from the regulation of body temperature by the animals depending on ". . . detection of deviations from a set point of some rate process bearing a direct exponential relation to body temperature. . . . Since physiological activity bears a direct exponential relation to temperature, the corresponding body-temperature distribution for the animals concerned would necessarily be negatively skewed." Speckled sanddabs, however, show a positively skewed mesokurtic distribution. A mesokurtic frequency distribution is not overly peaked (leptokurtic) or flat (platykurtic). Ivlev and Leizerovich (1960) and Ehrlich et al. (1979) used kurtosis to quantify the strength or precision of the preference: leptokurtic distribution indicates greatest preference.

The peak abundance of speckled sanddabs in King Harbor occurred from winter through spring and early summer when bottom temperatures were low (Figure 3). During the late summer and fall breakdown of stratification, warm bottom water was associated with a pronounced decrease in the number of fish observed. Stephens et al. (1974) found a similar decrease in abundance of speckled sanddabs during destratification in Los Angeles Harbor. Figure 3 also shows that the lower winter and early spring temperatures dur-

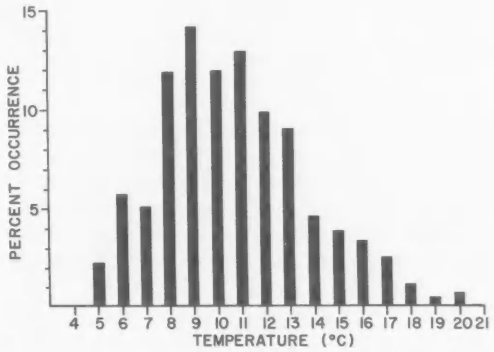

FIGURE 2.—Temperature-specific occurrences of speckled sanddabs, based on pooled data from 2,290 fish observations. The frequency distribution was significantly skewed toward warmer temperatures ($g_1 = 0.571$, $t_{99\,df} = 2.33$, $0.01 < P < 0.025$) but was mesokurtic, that is not overly peaked or flat ($g_2 = 3.078$, $t_{99\,df} = 1.59$, $0.1 < P < 0.2$).

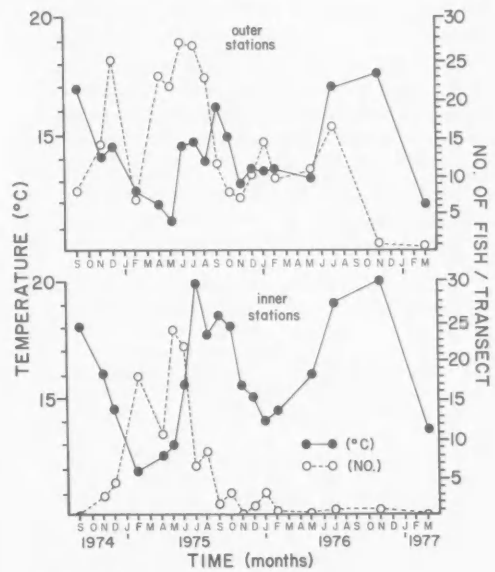

FIGURE 3.—Bottom temperatures and number of speckled sanddabs per transect at inner and outer stations in King Harbor, September 1974 to March 1977.

ing 1974, as compared with 1 yr later, coincided with a larger population of speckled sanddabs. The population density variability shown in Figure 3 results, at least in part, from the patchy distribution of the fish. Even at the time of year of greatest density the occasional transect found no fish. When fish were observed at these times of year, however, the numbers were high.

We grouped the abundance of speckled sanddabs per transect data according to the observed field temperature at the time of the survey to help explain the distribution of the fish (Table 2). The mean abundance per transect was determined for each observed field temperature (11°-20°C), and we calculated the percent occurrence at each temperature after correcting for the variation in occurrence of each temperature. This correction was accomplished by dividing the fish abundance at each temperature by the number of times the temperature occurred. We compared the temperature-specific field distribution with the temperatures selected in the laboratory by speckled sanddabs as a step in trying to understand the effect of temperature on field distributions. The laboratory data of temperature-specific occurrences was recalculated using only data for fish that were observed at 11°C or higher temperatures as if we had only sampled that part of the population occurring above 11°C (Figure 4). Statistical analysis of the arc sine transformed frequency distributions revealed no significant difference between laboratory and field data ($\chi^2_{9\,df} = 10.75$, $0.25<P<0.50$). We found a significant correlation between percent occurrence (arc sine transformed) and field temperature ($r_{8\,df} = -0.869$, $P<0.01$) of the data in Table 2. This high degree of correlation indicates that 76% ($r^2 \times 100$) of the variation in the field occurrence of speckled sanddabs in King Harbor seems explained by temperature. The similarity in temperature-specific distributions for the laboratory and field data (Figure 4) indicates that speckled sanddabs in King Harbor represented only that portion of the population found in warm water. Comparison of Figures 2 and 4 indicates that the greatest density of these fish may occur outside of the harbor in deeper, colder water. Furthermore, these fish in King Harbor do not appear to be a subpopulation endemic to this harbor. This would be in agreement with Taylor (1957) who suggested that there is but one popula-

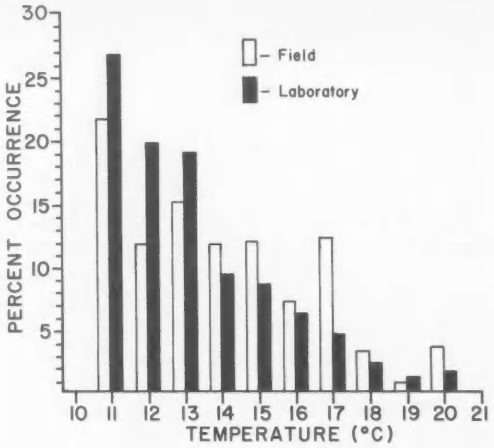

FIGURE 4.—Correspondence of temperature-specific occurrences of speckled sanddabs in the laboratory and field. The frequency distribution for the laboratory data was obtained from Figure 2 using only data for fish that occurred at 11°C or higher, which matched the range of observed field temperatures.

TABLE 2.—Frequency of occurrence of temperatures and speckled sanddabs in King Harbor, Redondo Beach, Calif.

Parameter	11°C	12°C	13°C	14°C	15°C	16°C	17°C	18°C	19°C	20°C
Temperature occurrences (X)[1]	1	5	6	9	3	5	2	5	1	2
Fish abundance (Y)[2]	21.8	18.0	24.0	4.2	1.2	2.7	8.0	0.0	0.8	6.5
		10.5	24.7	3.0	27.0	21.8	16.6	8.5		0.8
		7.0	7.0	0.7	7.8	0.2		1.5		
		23.0	10.3	0.0		0.5		3.0		
		0.5	14.5	14.0		11.5		1.0		
			10.8	25.0						
				27.3						
				22.8						
				9.5						
ΣY	21.8	59.0	91.3	106.5	36.0	36.7	24.6	14.0	0.8	7.3
$\Sigma Y/X$	21.8	11.8	15.2	11.8	12.0	7.3	12.3	2.8	0.8	3.6
% occurrence[3]	21.9	11.9	15.3	11.9	12.1	7.3	12.4	2.8	0.8	3.6

[1] X is number of surveys that occurred at the indicated temperature.
[2] Y is number of fish observed per transect during each survey that occurred at the indicated temperature.
[3] % occurrence = $\left[(\Sigma Y/X)/\Sigma(\Sigma Y/X)\right] \times 100$, where $\Sigma(\Sigma Y/X) = 99.4$. It is coincidental that this number approximates 100.

tion of speckled sanddabs over its entire open coast range.

Biotic and abiotic factors, in addition to temperature, must be considered when relating temperature preference data to field situations. Factors such as the presence of predators or prey, nutritive condition, light levels and/or physical substrate can influence the temperature selected under natural conditions (Fleming and Laevastu 1956; Brett 1970, 1971; Blackburn and Williams 1975; Beitinger and Magnuson 1975). Stephens (in press) reported that the speckled sanddab prefers sand (outer stations in King Harbor) rather than mud substrate (inner stations in King Harbor). These types of parameters are probably particularly responsible for the 22% variation in field occurrences that was not explained by temperature. In the laboratory where we controlled these variables, we found a higher correlation ($r_{8\,df} = -0.976$) between fish occurrence and temperatures, which accounted for 95% of the variation in fish position.

Based on the laboratory data, it appears that the water in King Harbor is usually warmer than that preferred by speckled sanddabs. This is particularly true if one considers the modal selected temperature (9°C). Reynolds (1977) suggested that the mode is the best indicator of fish's thermal preference. Occurrence of speckled sanddabs in King Harbor, where their modal preferred temperature was not observed on any of the surveys indicates that this harbor (particularly the inner part) may be a marginal area for this species. We observed a high rate of parasitism by the isopod *Livonica vulgaris* in King Harbor on speckled sanddabs (virtually 100% infection), compared with the lower levels (approximately 25% infection) observed in this species collected in La Jolla, Calif. (Ford 1965). This appears to support our hypothesis that this area may be of marginal value to speckled sanddabs and that they may be under stress and more susceptible to infection. Snieszko (1974) reported such a relationship between stress and infection for some fish species.

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MERCURY AND SELENIUM IN BLUE MARLIN, *MAKAIRA NIGRICANS*, FROM THE HAWAIIAN ISLANDS

In a previous study, nine species of pelagic and inshore fish caught in Hawaiian waters were analyzed for total and organic mercury (Rivers et al. 1972). In all but one species the organic mercury was >80% of the total, a finding consistent with other mercury values reported (Kamps et al. 1972; Westöö 1973). In muscle and liver tissues of blue marlin, *Makaira nigricans* Lacépède, however, only a small portion of the total mercury was found to be organic mercury. Additional studies on marlin landed during fishing tournaments in 1972 (Schultz et al. 1976) and 1973 (Schultz and Crear 1976) revealed low levels of organic mercury in six other tissues. These studies also showed that the difference between total and organic mercury was indeed inorganic mercury. G. Westöö (National Swedish Food Administration, Stockholm. Pers. commun., 1972) had previously identified the organic fraction as methyl mercury.

An assessment of mercury is complicated by the presence of selenium. Selenium has been shown to reduce the toxicity of mercuric chloride and methyl mercury in laboratory animals when given as selenite, selenomethionine, or as selenium present in tuna (Pařízek et al. 1971; Ganther and Sunde 1974). The presence of selenium in tuna, a principal food item of marlin (Naughton[1]), indicates that it should also be present in marlin.

For this report, nine tissues from blue marlin were analyzed for selenium, total mercury, and organic mercury.

Materials and Methods

Samples of muscle, liver, kidney, spleen, pyloric caecum, stomach, gill, gonad, and blood were collected from 46 marlin landed during a fishing tournament in Kailua-Kona, Hawaii, during August 1974. The tissues were ground with Dry Ice[2] in a blender and stored in acid-washed plastic vials.

The organic extraction was carried out as described by Rivers et al. (1972), i.e., a benzene extraction of the methyl mercury was reextracted with cysteine, oxidized with permanganate, and reduced to elemental mercury with stannous ion prior to being volatilized into the flameless atomic absorption apparatus. Total mercury digestions were performed (Rivers et al. 1972) but with 10 ml of concentrated nitric acid instead of 30 ml. All analyses were made with a Perkin-Elmer 303 atomic absorption spectrophotometer equipped with a vapor chamber (Manning 1970).

Selenium was determined by a fluorometric technique (Watkinson 1966), as modified by S. Nishigake (Tokyo Metropolitan Research Laboratory of Public Health, Tokyo, Japan. Pers. commun., 1975), i.e., following sample digestion with nitric and perchloric acids, the selenium was complexed with 2,3-diaminonaphthalene and this fluorescent compound then extracted into cyclohexane. All analyses were made using a Turner Model 110 fluorometer equipped with a primary filter at 369 nm and a secondary filter at 522 nm.

[1]Naughton, J. J. 1973. To all billfishermen. (Summary report of 15th Hawaiian International Billfish Tournament, 27-31 August 1973), 9 p. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

A summary of mercury and selenium concentrations in the marlin is given in Table 1. Average total mercury and selenium values were greatest in kidney (26.33 mg/kg Hg, 23.42 mg/kg Se) and least in blood (0.18 mg/kg Hg, 1.29 mg/kg Se) and gill (0.32 mg/kg Hg, 1.29 mg/kg Se). Average methyl mercury was highest in muscle (0.40 mg/kg) and lowest in blood (0.04 mg/kg) and gill (0.06 mg/kg). The percentage of organic to total mercury ranged from 1% in kidney to 27% in gonad. The molar ratio of mercury to selenium ranged from 0.06 in blood to 0.62 in muscle. (Molar ratio is computed here using sample average statistics of combined male and female data.)

An analysis of variance revealed significant differences ($P<0.05$) in total mercury between males and females for all tissues except gill and blood. A similar pattern was found for selenium. The organic mercury levels were not statistically different ($P>0.05$) between the sexes. In earlier studies on marlin caught from the same area during fishing tournaments in 1971, 1972, and 1973, mercury concentrations in both sexes were found to be similar.

Table 2 presents correlation coefficients for body weight and tissues. In most cases, the relationships are positive and highly significant. Figures 1-6 illustrate the dependence of mercury and selenium on weight and on each other.

Discussion

The data clearly demonstrate that methyl mercury concentrations are low relative to total mercury in blue marlin. Westöö (pers. commun.) and Nishigaki (pers. commun.) confirmed this low percentage in our samples based on subsamples sent to them. Nishigaki has also confirmed our selenium results.

In a study of 37 Pacific blue marlin (50-238 kg, average 109 kg) from Japanese waters, Nishigaki (pers. commun.) found total mercury levels ranging from 0.02 to 13.0 mg/kg (average 2.83 mg/kg) and methyl mercury ranging from 0.02 to 1.28 mg/kg (average 0.57 mg/kg). Selenium values for 11 marlin ranged from 0.52 to 1.99 mg/kg, averaging 0.97 mg/kg. These values are similar to our findings for mercury and selenium in marlin from Hawaiian waters.

TABLE 1.—Summary of mercury and selenium data in 46 blue marlin from the Hawaiian Islands by sex.[1]

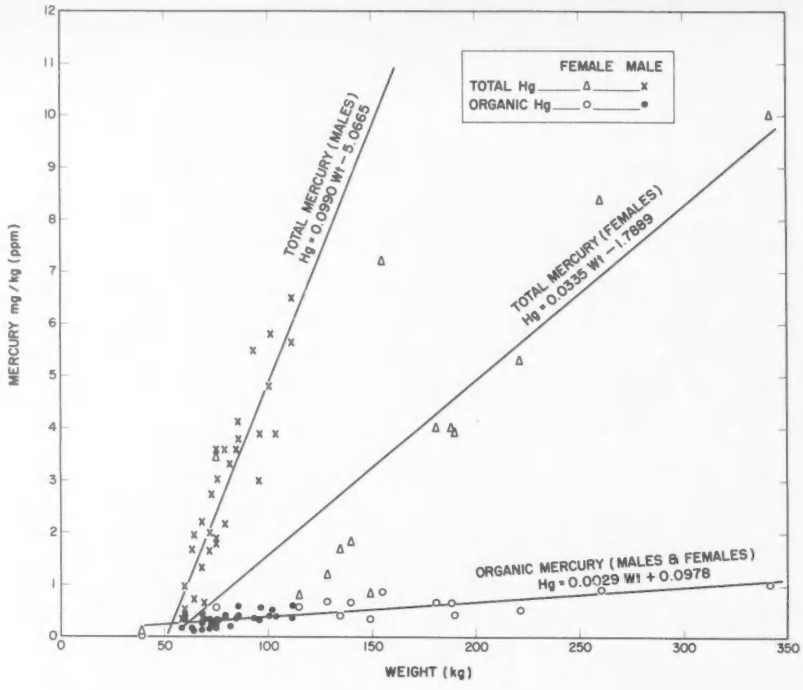
	Total Hg (mg/kg)				Organic Hg (mg/kg)				% organic Hg of total Hg	Se (mg/kg)				Hg/Se molar ratio
	Mean			Range	Mean			Range		Mean			Range	
Tissue	M & F	M	F	M & F	M & F	M	F	M & F	M & F	M & F	M	F	M & F	M & F
Muscle	3.12	2.83	3.76	0.09-10.00	0.40	0.32	0.58	0.02-1.02	13	1.98	1.88	2.21	0.63-5.32	0.62
Liver	11.58	12.53	9.46	0.13-39.20	0.26	0.21	0.38	0.09-0.76	2	17.47	20.36	11.06	2.50-61.12	0.26
Kidney	26.33	26.25	26.53	0.18-77.00	0.22	0.16	0.35	0.04-0.86	1	23.42	25.33	19.06	2.63-56.25	0.44
Spleen	6.93	6.34	8.21	0.08-17.60	0.18	0.12	0.30	0.02-0.66	3	9.31	9.12	9.73	0.63-24.25	0.29
Stomach	1.27	1.33	1.16	0.06-3.00	0.12	0.08	0.21	0.03-0.47	9	2.91	3.16	2.39	1.35-4.03	0.17
Pyloric caecum	1.83	1.74	2.03	0.17-4.50	0.30	0.22	0.49	0.08-0.98	16	4.92	5.10	4.52	2.28-10.10	0.15
Gill	0.32	0.26	0.44	0.08-0.96	0.06	0.03	0.11	<0.01-0.34	19	1.29	1.31	1.26	0.71-2.21	0.10
Gonad	0.40	0.30	0.68	0.03-2.15	0.11	0.06	0.25	0.03-0.65	27	2.14	1.97	2.60	1.24-3.80	0.07
Blood	0.18	0.18	0.18	0.02-0.53	0.04	0.04	0.05	<0.01-0.11	22	1.29	1.33	1.19	0.72-2.30	0.06

[1]Weights of 32 males ranged from 58 to 112 kg (average 80); 14 females weighed 39, 75, and 115-342 kg (average 166). Average for all samples was 106 kg.

TABLE 2.—Correlation coefficient of mercury, selenium, and weight in 46 blue marlin from the Hawaiian Islands by sex.

	Total Hg/wt			Organic Hg/wt	Organic/ total Hg	Se/wt			Total Hg/Se	Organic Hg/Se
Tissue	M & F	M	F	M & F	M & F	M & F	M	F	M & F	M & F
Muscle	0.69**	0.90**	0.83**	0.79**	0.72**	0.68**	0.88**	0.85**	0.93**	0.61**
Liver	0.23	0.76**	0.69**	0.76**	0.13	0.00	0.68**	0.38	0.80**	−0.08
Kidney	0.49**	0.83**	0.79**	0.87**	0.42**	0.32*	0.79**	0.73**	0.91**	0.30*
Spleen	0.61**	0.88**	0.75**	0.84**	0.51**	0.45**	0.72**	0.61*	0.87**	0.41**
Stomach	0.38*	0.77**	0.82**	0.81**	0.35*	−0.27	0.18	0.15	0.32*	−0.33*
Pyloric caecum	0.59**	0.83**	0.82**	0.86**	0.59**	−0.11	0.32	−0.10	0.25	−0.14
Gill	0.86**	0.70**	0.90**	0.88**	0.77**	0.04	0.08	0.16	0.21	−0.14
Gonad	0.85**	0.75**	0.95**	0.82**	0.76**	0.15	−0.10	−0.53	0.10	0.25
Blood	0.28	0.32	0.57*	0.36*	0.44**	−0.04	−0.17	0.49	0.44**	0.09

*$P<0.05$.
**$P<0.01$.


FEMALE MALE
TOTAL Hg
ORGANIC Hg
TOTAL MERCURY (MALES)
Hg = 0.0990 Wt - 5.0665
TOTAL MERCURY (FEMALES)
Hg = 0.0335 Wt - 1.7689
ORGANIC MERCURY (MALES & FEMALES)
Hg = 0.0029 Wt + 0.0978
MERCURY mg / kg (ppm)
WEIGHT (kg)

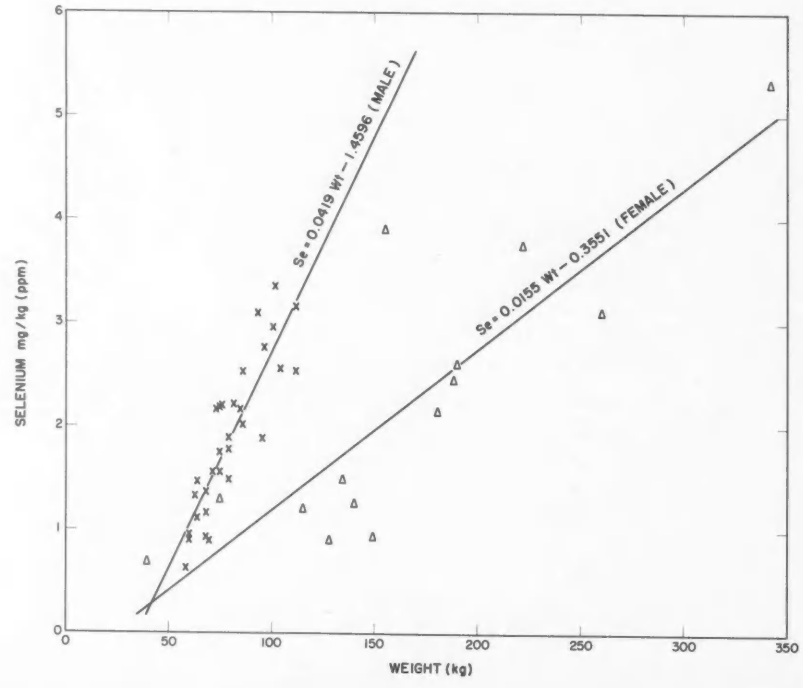

Se = 0.0419 Wt - 1.4596 (MALE)
Se = 0.0155 Wt - 0.3551 (FEMALE)
SELENIUM mg/kg (ppm)
WEIGHT (kg)

FIGURE 1.—The relationship of total and organic mercury in muscle tissue of 46 blue marlin from the Hawaiian Islands to fish weight.

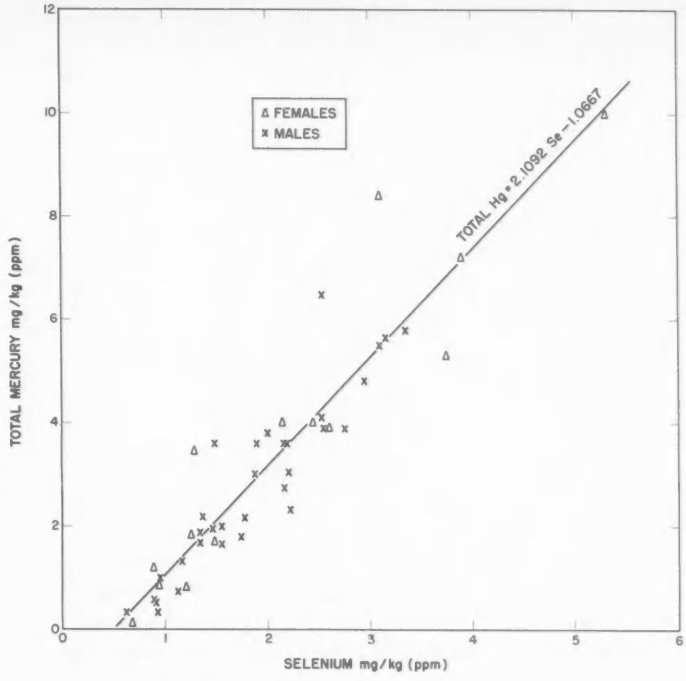


FIGURE 3.—Relationship between total mercury and selenium in muscle tissue of 46 blue marlin from the Hawaiian Islands.

FIGURE 2.—Relationship between selenium in muscle tissue and weight of 46 blue marlin from the Hawaiian Islands.

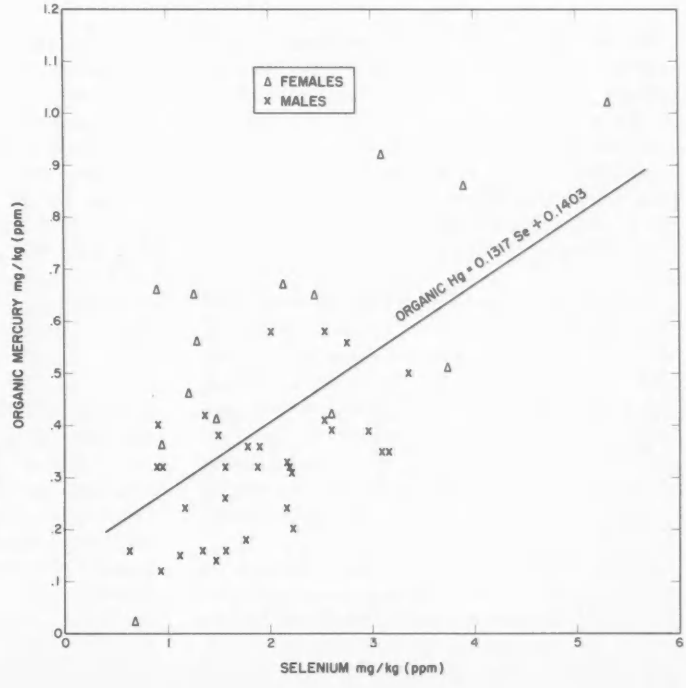


FIGURE 4.—Relationship between organic mercury and selenium in muscle tissue of 46 blue marlin from the Hawaiian Islands.

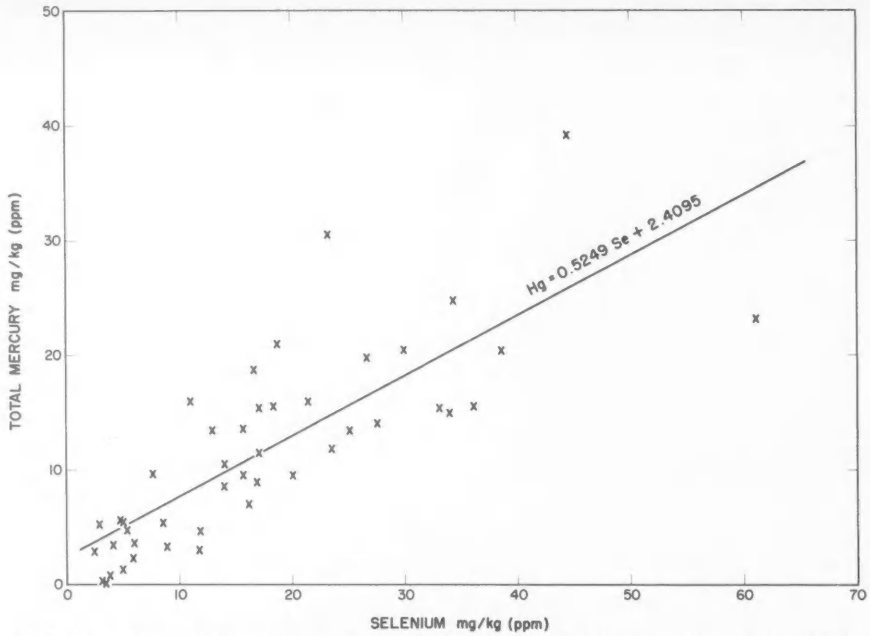


FIGURE 5.—Relationship between total mercury and selenium in liver of 46 blue marlin from the Hawaiian Islands.

Concentration through the food chain is apparently the reason for the elevated levels of mercury found in the marlin. Stomach contents examined in 76 blue marlin captured in 1973 showed that the most common food items were tuna, mostly *Katsuwonus pelamis* (38% occurrence); mackerel scad, *Decapterus pinnulatus* (36%); squid (21%); spiny puffer, Diodontidae (19%); and dolphin, Coryphaenidae (12%) according to Naughton (see footnote 1).

Mercury levels were reported for yellowfin tuna, *Thunnus albacares*, 0.54 mg/kg; skipjack tuna, *K. pelamis*, 0.38 mg/kg; and for dolphin, *Coryphaena hippurus*, 0.25 mg/kg; by Rivers et al. (1972). These are pelagic species and as such, are exposed to the same amount of mercury in their physical environment; yet all have mercury levels nearly an order of magnitude less than that of the marlin. In addition, their mercury content was essentially all methyl mercury.

If most of the mercury entered the marlin via the food chain as methyl mercury it would seem that demethylation to inorganic mercury had occurred. Conversion of methyl mercury to inorganic mercury has been shown to occur in bluegill (Burrows and Krenkel 1973) and in rats (Norseth and Clarkson 1970).

It is indicated in Figure 1 that the mercury is accumulated with size but at different rates for males and females. This observation contrasts with previous year's results in which no sex-related concentration disparities were found (Shultz and Crear 1976; Shultz et al. 1976). The reason for this year's anomaly is unclear and not enough information is available to determine if we are dealing with more than one population.

Selenium levels in the marlin are presented in Table 1 and show an increase with weight and age (Figure 2). The high correlation of mercury and selenium with weight (Table 2), and the observation that selenium modifies the activity of mercury in experimental animals, indicate that they are highly correlated with each other, as is seen in Figures 3-6. The precise nature of the mercury-selenium interaction is not known, although a number of suggestions have been advanced. Parízek et al. (1971) demonstrated with rats that the protective effect of selenite against mercuric chloride was not related to an increase in mercury excretion but to a decrease, resulting in a change

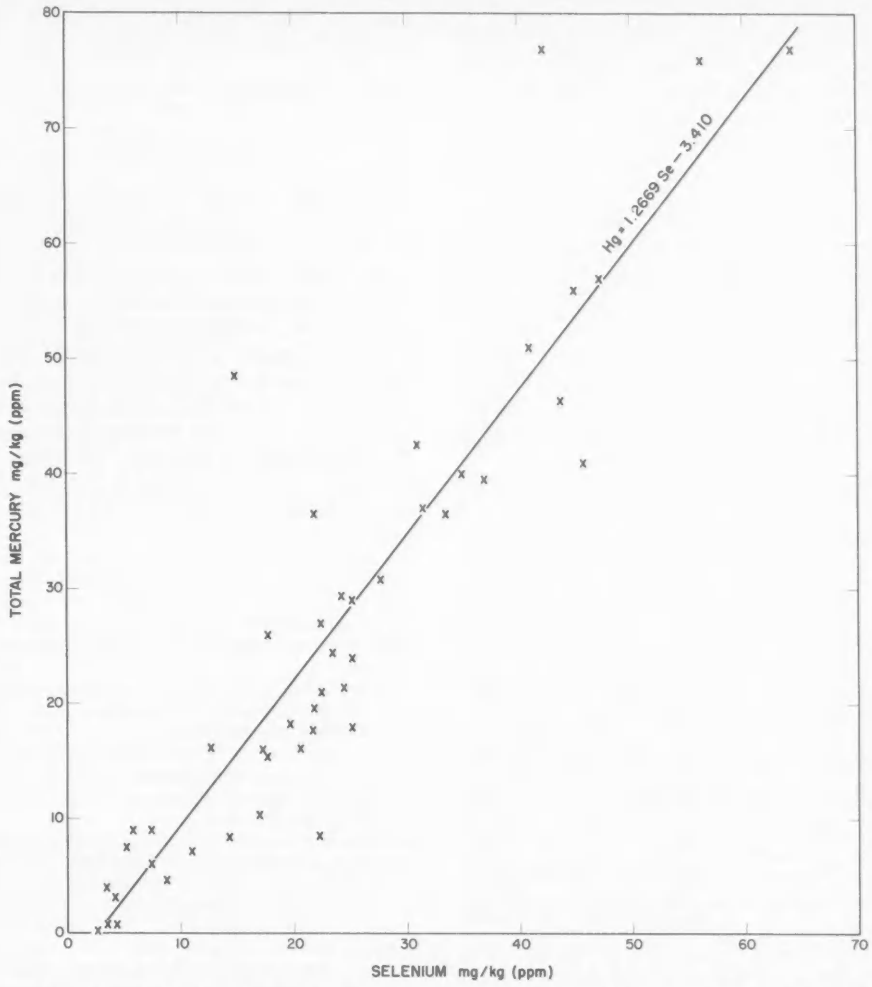


FIGURE 6.—Relationship between total mercury and selenium in kidney of 46 blue marlin from the Hawaiian Islands.

in organ distribution of mercury. The kidneys and intestines lost mercury while the testes gained mercury relative to the controls. In addition, mercury in the macromolecular fraction of blood plasma increased after addition of selenite. Burk et al. (1974) found a similar increase of mercury in plasma protein when mercuric chloride was administered simultaneously with selenite. This was not the case when mercuric chloride or selenite was injected alone. Their experiments using dialysis of rat plasma protein indicated that selenium and mercury are bound in a 1:1 molar ratio to a single protein, with selenium attached to the protein through a sulfhydryl group and mercury attached to the selenium. They also observed a time lag after injection of selenite before detection of protein binding during which the selenite was apparently metabolized to another form. Lunde (1970) has found selenium to be associated also with proteins in marine organisms.

The molar ratio of average total mercury to average selenium in muscle is 0.62. Subtracting the methyl mercury to obtain inorganic mercury (Schultz and Crear 1976), the ratio reduces to 0.54.

Ganther et al. (1972) reported that the mercury to selenium molar ratio for high-mercury tuna (can tuna) (average 2.87 mg/kg) approaches 0.5. They also noted that the mercury and selenium increments between low-mercury tuna (0.32 mg/kg) and high-mercury tuna were about in a 1:1 molar ratio, implying they are accumulated together.

The total mercury-selenium relationships observed in marine mammals and man are similar to those found in tuna. Koeman et al. (1973) found a 1:1 molar ratio in the livers of seals, *Phoca vitulina*, porpoises, *Phocoena phocoena*, and dolphins, *Tursiop truncatus*, *Delphinus delphis*, *Lagenorhynchus obscurus*, and *Sotalia guianensis*. Regression analyses of their data give an average slope of 2.7 ± 0.2 or 1.1 ± 0.1 on a molar basis for mercury-selenium interactions ($r = 0.932$). Interestingly, they found that only 2 to 14% of mercury in the liver and 2 to 13% in the brain was recovered as methyl mercury. Post-mortem studies on humans exposed to high inorganic mercury (from a mercury mine) showed a 1:1 molar ratio of mercury to selenium ($r = 0.998$) in tissues which had accumulated high amounts of mercury, i.e., thyroid, pituitary, kidney, and brain (Kosta et al. 1975). They noted, however, that this ratio did not exist for a nonexposed group in which mercury and selenium levels were insignificant. Elevated mercury levels were apparently responsible for increasing the selenium concentrations such that, in many cases, the molar ratio of mercury to selenium increments over normal levels approached 1:1 (selenium was low in the mine environment: 1 mg/kg versus 100 mg/kg Hg—in contrast to the relative enrichment of selenium in the diet of tuna and marine mammals). The levels of methyl mercury in organs of the exposed group were low, implying that no significant in vivo methylation occurs in man.

Because selenium is high in the marlin (average 1.98 mg/kg in muscle, 17.47 mg/kg in liver, 23.42 mg/kg in kidney), the possibility of selenium toxicity should not be discounted. Aptly, though, mercury has been shown to mitigate the toxicity of selenium in rats and chicks (Pařízek et al. 1971; Hill 1974).

In an earlier study, it was indicated that cooking did not remove either methyl or total mercury from marlin fillets (Schultz and Crear 1976). Higgs et al. (1972) have found that baking does not remove selenium from flounder or chicken although some loss was reported from boiling two vegetables. It does appear then that mercury (muscle average 3.12 mg/kg) and selenium (muscle average 1.98 mg/kg) concentrations in raw fillet are representative of that in cooked fish.

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RECENT RECORDS OF *CALLINECTES DANAE* AND *CALLINECTES MARGINATUS* (DECAPODA: PORTUNIDAE) FROM NORTH CAROLINA WITH ENVIRONMENTAL NOTES

Temperature and latitudinal distributions of the genus *Callinectes* are best known for *C. sapidus* Rathbun (Williams 1974; Norse 1977). The northern limits of *C. danae* Smith and *C. marginatus* A. Milne Edwards are listed as Bermuda and southern Florida, with one specimen of *C. marginatus* from North Carolina regarded as a temporary range extension (Williams 1974). We report the taking of two specimens of *C. danae* and six specimens of *C. marginatus* by 12.2-m (40-ft) otter trawl in and near the Cape Fear River estuary, N.C. All specimens have been deposited at the Institute of Marine Sciences, University of North Carolina, Morehead City, N.C. Measurements listed are of carapace width in millimeters including lateral spines.

Two specimens of *C. danae* (UNC 2766, ♂ 115; ♂ 113), 1 *C. marginatus* (UNC 2765, ♂ 97), 6 *C. ornatus* Ordway, and 7 *C. similis* Williams were captured by trawl in the Intracoastal Waterway on 19 September 1977, just south of the Carolina Beach Inlet, on a sand-shell bottom 4 m deep in water of 36‰ surface salinity and 26°C. Four *C. marginatus* (UNC 2763, ♀ 92; ♂ 103; ♂ 62; ♂ 81) were also caught at this location on 14 September 1977, along with 30 *C. ornatus*, 35 *C. similis*, and 10 *C. sapidus*. Bottom salinity was 20‰, and bottom temperature was 26.5°C. Several other small specimens of *C. marginatus* (40-60 mm) were observed, but not retained in this trawl. A sixth specimen of *C. marginatus* (UNC 2764, ♀ 91), 1 *C. ornatus*, 30 *C. similis*, and 20 *C. sapidus* were collected in the intake canal of the Carolina Power and Light Company generating plant in the Cape Fear River estuary west of buoy 19 on 11 October 1977. Bottom type was silty-sand at depth of 4 m. Surface salinity was 31‰ and surface water temperature was 17°C.

The present record of *C. danae* represents a northward range extension of 1,000 km, from Biscayne Bay, Fla., to the Cape Fear River. Williams (1974) noted that it occurs in a wide range of salinities and habitats. However, Norse (1977) believed *C. danae* prefers lower salinities, from studies in the Caribbean.

The six specimens of *C. marginatus* bring the total recorded in North Carolina and north of southern Florida to seven. Shallow environments over a wide range of substrates are preferred in a salinity range of 19-32‰ and temperature range of 22°-30°C (Williams 1974). Norse (1974) has inferred a preference for higher salinities by *C. marginatus*; note, we obtained four of the six specimens at 20‰ and a fifth was captured inside the Cape Fear estuary where salinities fluctuate widely.

Callinectes danae, *C. marginatus*, and *C. ornatus*, with the exception of two specimens of the latter from Charleston, S.C., are now recorded from Florida, North Carolina, and Bermuda. Another species which occurs in Florida and Bermuda, *C. exasperatus* Gerstaecker, has yet to be taken in

North Carolina. The northerly distribution for these species may be indicative of larval transport patterns via currents, i.e., Gulf Stream (Williams 1974). Another significant element, as proposed by Norse (1977), is the presence of summer temperatures in excess of 20°C required for the hatching of eggs and larval development.

Acknowledgments

We express appreciation to Austin B. Williams for his confirmation of the *C. marginatus* specimens, and Elliott A. Norse for his identification of the *C. danae* specimens. The study was funded by Carolina Power and Light Company.

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ANALYSIS OF CHLORINATED HYDROCARBON POLLUTANTS: A SIMPLIFIED EXTRACTION AND CLEANUP PROCEDURE FOR FISHERY PRODUCTS

Fishery scientists wishing to quantitate chlorinated hydrocarbons find a multitude of methods only marginally appropriate to the routine analysis of marine fishery products. This paper is a laboratory manual, delineating details of a simple, rapid, and reliable method for the extraction and cleanup of samples of fish, fishery products, and paper for analysis of chlorinated hydrocarbons, such as PCB,[1] dieldrin, and DDT and its metabolites TDE and DDE. The procedures can be adapted to a great variety of sample types. The method is economical since small amounts of solvents are used and the equipment and glassware are relatively inexpensive and readily available.

Chlorinated hydrocarbon analysis in marine fishery products is an extremely complex procedure requiring extensive knowledge and many years of experience to perfect. A number of specialized problems, uncommon in the preparation of foodstuffs and freshwater fish for analyses of chlorinated hydrocarbons by the established methods, occur during the isolation of such materials from marine fish and fishery products. For example, the official method of the Association of Official Analytical Chemists (Horowitz 1970; Porter et al. 1970) often requires 1½ days for the initial extraction of marine fish oil because of intractable emulsions. After purification, the final extracts still contain substances which cause the rapid loss of sensitivity of the electron-capture detector and decomposition of the column packing in the gas-liquid chromatographic system. The procedure described in this paper eliminates extraction of fish oil and provides final extracts freer of extraneous substances. In the course of analyzing over 2,000 samples we have found it suitable for routine analysis of marine fishery products.

The method was first developed by Robert Reinert (Reinert 1970; Snyder and Reinert 1971). We have refined it to maximize recovery of chlorinated hydrocarbons and have adapted it to new types of samples, such as fishmeal and carbonless carbon paper. We have described the procedure in detail because of the ultimate purity and freedom from unanticipated contaminants required of extracts for gas chromatography with an electron-capture detector. Data from samples of typical fishery products analyzed by us using the methods described in this paper were comparable to the data obtained by a number of other laboratories[2] following their usual procedures.

Preliminary Information

The accuracy and precision of analyses for chlorinated hydrocarbons are assured only if careful attention is given to the procedural details and the time factors involved in the various steps.

[1]Abbreviations used in this paper: DDE—*p, p'*-dichlorodiphenyldichloroethylene; DDMU—*p, p'*-dichlorodiphenylchloroethylene; DDT—*p, p'*-dichlorodiphenyltrichloroethane; IPA—isopropyl alcohol; PCB—polychlorinated biphenyls (Aroclor 1254 was used as the standard for PCB); and TDE—*p, p'*-dichlorodiphenyldichloroethane. The *o, p'*-isomers of DDT and its metabolites act similarly to the more common *p, p'*-isomers used here.

[2]See Acknowledgments for the list of laboratories.

Time

For a set of eight samples: Extraction of oil, none; extraction of other samples, 4 h (or less); cleanup, 1 h; separation of DDT and PCB, 4 h; and transfer and dilution of samples for gas-liquid chromatography, 1-2 h.

Reagents

Analytical standards: U.S. Environmental Protection Agency, Health Effects Research Laboratory, Environmental Toxicology Division, Research Triangle Park, N.C.

Aroclor[3]1254: Monsanto Company, St. Louis, Mo. (Aroclor 1254 was used as the analytical standard for PCB because it represented the PCB most typically found in our samples. Snyder and Reinert (1971) tested both Aroclor 1254 and Aroclor 1260. The suitability of the procedure for PCB of other degrees of chlorination would need to be verified.)

Sodium sulfate: anhydrous, reagent grade. If the blank indicates the sodium sulfate is contaminated, rinse with petroleum ether or hexane and dry before use.

Solvents: distilled-in-glass grade, Burdick & Jackson, Muskegon, Mich. (The suitability of other "pesticide" or "nanograde" solvents would need to be determined.)

Florisil: 60/100 mesh P.R. grade, Floridin Company, Pittsburgh, Pa. Store in the dark in tightly closed, screw-cap, flint glass jars, and use without further activation.

Silica gel: grade 950, 60/200 mesh, desiccant, Davidson Division, Grace Chemical Company, Baltimore, Md. (The performance of other silica gels would have to be evaluated.)

Carborundum chips: 16 mesh. Use as a boiling aid in all evaporation steps. (Whenever ebullition is interrupted, new chips are necessary.)

Aluminum foil: domestic grade.

Teflon wash bottles: Nalgene Co., Rochester, N.Y. Use for adding small amounts of solvents in the boildown and chromatographic procedures. Discard the contents of the wash bottle if left longer than a day.

Glassware

Glassware: borosilicate (DDT and TDE decompose on contact with flint glass).

Glass wool: borosilicate fiber glass, Corning 3950 or equivalent. Use directly from the package.

Graduated centrifuge tubes: 50-ml, Kimax 45164 or equivalent, and stoppered 13-ml, K-410550, Kontes Glass Co., Vineland, N.J., or equivalent.

Modified micro Snyder column: Kontes K-569251 or equivalent.

Chromatographic columns: 7 mm i.d. × 150 mm and 9 mm i.d. × 150 and 250 mm glass tubing. (All tubes are without stopcocks.)

Storage bottles: 23-ml screw-cap, borosilicate specimen bottles, Prescription Containers, Inc., Brooklyn, N.Y., with Teflon cap liners, 2390-H62, Arthur H. Thomas Co., Philadelphia, Pa.

Pipettes: Class A. Use for preparation of standards.

Pipettes: disposable glass. Use for quantitative dilution and transfer of samples.

Pipettes: disposable glass, Pasteur capillary, Kimax 72000 or equilavent. Use for sample transfer. (Disposable pipettes are preferred for handling samples in order to eliminate cross contamination.)

Equipment

Virtis homogenizer: Macro, Model 23 or 45, with stainless steel blades, Teflon cap, and 10-50 ml glass homogenizer flasks (No. 16-207), Virtis Co., Gardiner, N.Y., or equivalent. (Bearing lubricants contaminate samples.)

Tube heater: Kontes K-720000. (It is convenient for evaporating solutions in 13-ml centrifuge tubes.)

Plastic and Rubber

Avoid materials, such as gloves, flexible tubing, and polyethylene bags, which often contain PCB or substances which interfere with quantitation by gas chromatography with an electron-capture detector. (Teflon is the only plastic suitable for these analyses.) Wrap samples in aluminum foil for shipment to the laboratory.

Washing Procedure

Chlorinated hydrocarbons and some of the substances in samples adhere tenaciously to glassware. To prevent contamination of future samples, rinse glassware with an organic solvent immediately after use, and then soak in water until washing.

[3]Mention of trade names or companies does not imply endorsement by the National Marine Fisheries Service, NOAA.

Wash all glassware (and spatulas) in the hottest water practical and rinse thoroughly also with very hot tapwater. (Unless an all-glass still and piping system is available, tapwater is preferable to distilled water because stills often contain plastic tubing and sealing compounds containing PCB.) Bake glassware overnight at 225°-250°C to reduce residual contamination. Cover glassware with aluminum foil. Rinse 3-5 times with petroleum ether or hexane immediately before use. Keep containers covered with foil or stoppers except during evaporation or chromatography to exclude dust, etc.

Procedure For DDT and PCB

The details in time and quantity of chemicals are given only as general guidelines. The exact parameters of these procedures vary with ambient temperature, humidity, altitude, etc. They must be adjusted in each laboratory to optimize recovery, cleanup, and separation of desired components.

Caution

All procedures involving benzene must be performed in a well-functioning hood.

Blank

Carry out the complete procedure as described below without any test sample (omit step 1 under Extraction) to assure that the blank is substantially below the level to be determined. Evaporate the final solutions to 2 ml and quantitate the residues, typically <0.001 ng/μl DDT, TDE, and DDE and <0.01 ng/μl PCB. (Incompletely washed glassware and new batches of reagents are common sources of high blanks.)

Recovery

Carry out the complete procedure with solutions of standards of known concentration in the range anticipated for the samples to assure quantitative recovery. (Some loss of chlorinated hydrocarbons always occurs in the absence of proteins and lipids, which act as keepers. A minimum recovery of 80% is essential. Doping samples originally containing very low levels of chlorinated hydrocarbons gives results which better reflect the accuracy of the method: 85% or higher recovery of DDE, TDE, DDT, and PCB, and 80-85% recovery of dieldrin and endrin.)

Extraction

1) Weigh approximately 10 g of the material (see Procedure Variations for exceptions), to be analyzed into a Virtis flask and record exact weight to the desired degree of accuracy.

2) Add 20 ml of a 1:1 IPA/benzene mixture to the flask.

3) Homogenize at about 23,000 rpm for 5 min.

4) Rinse homogenizer blade and Teflon cap with hexane so that the hexane drips into the Virtis flask. Fill the flask with hexane nearly to the bottom of the flask neck.

5) Place the Virtis flask in a hot-water bath (ca. 85°C) or sand bath. (An electric fry pan with a layer of sand covered with water provides an economical heating bath.) Boil moderately for at least 45 min, adding hexane whenever the level falls to about one-third of the flask capacity. (If the solution boils too rapidly, material will be lost in the spray. The rate of boiling must be adequate to distill all the H_2O, IPA, and benzene from the flask, because they interfere with the cleanup.) When adding hexane, do it so as to rinse down the sides of the flask as well. Keep the water level in the bath and the hexane level in the flask adjusted so that the flask does not become buoyant and tip over. After 45 min of boildown, reduce the volume of the solution to about 20 ml (ca. 1 cm from the bottom of the flask). Cool. If a layer of water separates, add Na_2SO_4 and allow to stand 1-3 min.

6) Filter through a funnel plugged with glass wool into a 50-ml graduated centrifuge tube. Rinse the flask with three or four 5-ml portions of hexane and pour the rinse solutions through the filter into the centrifuge tube.

7) Concentrate the extract in a hot-water bath to desired volume (20-25 ml), record volume, and pour most of extract into a 23-ml borosilicate screw-cap bottle (with Teflon-lined cap) containing 1 g Na_2SO_4. (The extract can be stored in this condition for extended periods.) (If the extract, prior to concentration, still contains traces of H_2O or IPA, as indicated by cloudiness, add hexane while concentrating in order to remove the H_2O or IPA.)

Oil Determination

8) Pipette exactly 1 ml of the extract into a tared aluminum weighing dish and allow it to

evaporate 4-6 h at room temperature to minimum weight. (Since marine oils oxidize, the weight of oil begins to rise again after a few hours.) Weigh the residue, which contains the oil in 1 ml of extract.

Cleanup

9) Prepare a Florisil column by filling a 9 mm i.d. × 150 mm glass tube, plugged with glass wool, with ca. 5 cm of Florisil. Wash the column with at least 15 ml of hexane added 1 ml at a time. Allow the hexane level to drop to 1-2 mm, but not to dryness. Pipette 1 ml of the extract onto the column. For samples with very high oil content (refer to step 8 for the amount of oil in 1 ml of the extract), adjust the volume placed on the Florisil so that no more than 0.1 g, and preferably no more than 0.08 g, of oil is placed on the Florisil. Elute with 1-ml portions of hexane; collect the first 12-13 ml of the eluate in a 13-ml graduated centrifuge tube. (Note: Once the Florisil has been wetted, it must always have solvent above it.)

10) If DDT and PCB are not going to be separated, concentrate (in a tube heater) the eluate to an appropriate volume for gas-liquid chromatographic analysis.[4] If separating DDT and PCB, evaporate the eluate to slightly less than 1 ml.

Separation of DDE, TDE, and DDT from PCB

Quantitation of TDE and DDT is often difficult and quantitation of the PCB is usually impossible unless the DDT family is separated from the PCB. Separation is achieved by chromatography on silica gel. The behavior of DDT and PCB during solid-liquid chromatography is very similar, and obtaining optimal separation requires careful control of all the parameters of the procedure. Even so, DDE does not separate entirely from PCB. Therefore, the DDE in the PCB fraction is quantitated[5] and included with that in the DDT fraction.

Evaluate the degree of separation of DDE, TDE, and DDT from PCB by chromatographing standard solutions of these compounds according to the procedure described below. Adjust the time and temperature of activation, the degree of rehydration, the amount of silica gel, and the volume of the pentane fraction to obtain the optimum separation of DDT and TDE from PCB: that is, to maximize the amount of PCB in the pentane fraction and the amount of DDT and TDE in the benzene fraction.

11) Activate the silica gel by heating at 215°C for 16 h. (The time and the temperature are adjusted to obtain an arbitrarily, but consistently activated product with suitable separating characteristics, since complete dehydration occurs over a long period of time.) Cool to room temperature in a desiccator. Rehydrate by placing 98 g silica gel in a glass-stoppered bottle and adding 2 g distilled water. Stopper the bottle and shake and tumble until the water is evenly distributed. Allow the silica gel to equilibrate for 2-4 h before use.

12) Place a portion of this prepared silica gel in a beaker and cover with pentane. Let stand 5-10 min to return to room temperature. (Because the chromatographic columns do not contain stopcocks, a special technique is required for packing.) Quickly transfer silica gel to a glass-wool-stoppered column, 9 mm i.d. × 250 mm long, wet with pentane. (A disposable transfer pipette with the narrow part of the tip removed works quite well for transferring the silica gel slurry.) Tap the column gently to facilitate packing. Make sure that there is always enough pentane above the column to allow the silica gel to settle slowly in order to eliminate air bubbles and prevent the top of the column from running dry. Pack the column to a height of ca. 8 cm. (Throughout the whole separation procedure the silica gel must always have solvent above it and must be free of bubbles and cracks, which interfere with the desired separation. If the column runs dry or cracks, discard it.) Rinse the column with 15-20 ml of pentane.

13) Allow the pentane level to descend to 1-2 mm (not dry) and place the Florisil eluate (ca. 1 ml) on the column with a Pasteur capillary pipette. Rinse the Florisil eluate tube with three or four 1-ml portions of pentane, and transfer each rinse successively to the column. After the sample and rinses have been adsorbed, fill the tube with

[4]For a detailed description of gas chromatography of chlorinated hydrocarbon pollutants, see the Pesticide Analytical Manual (1977), available from Management Methods Branch, DMS, ACA, HFA-250, 5600 Fishers Lane, Rockville, MD 20857, or National Technical Information Service (NTIS), Springfield, Va. The manual provides extensive background on residue analysis.

[5]Although DDE elutes from the gas-liquid chromatograph at the same time as one of the PCB peaks, measurement of the other five intense PCB peaks provides accurate quantitation of PCB. Use the amount of PCB in those peaks to determine the size of the peak overlapping the DDE and correct the apparent total DDE (actually DDE plus PCB) to obtain the true DDE concentration. The electron-capture detector is so much more sensitive to DDE than PCB, that the correction affects the accuracy of DDE determination only to a small extent. Consequently the variability in amount of DDE in the pentane fraction does not markedly affect the accuracy of DDE analysis.

pentane. Collect 42 ml of pentane eluate in a 50-ml graduated centrifuge tube. (This fraction contains PCB and some DDE.)

14) After the appropriate volume of pentane eluate has been collected, place a second 50-ml graduated centrifuge tube under the silica gel column. Then fill the tube with benzene. Collect 35 ml of benzene eluate. (This fraction contains most of the DDT complex.) (DDE elutes very rapidly with benzene. If benzene is added to the column before the second centrifuge tube is in place, the DDT complex will often be found in the pentane fraction.)

15) Concentrate each fraction in a boiling water bath to less than the desired final volume and quantitatively transfer with hexane to a volumetric flask of the desired final volume. (The 50-ml centrifuge tubes are not very accurate volumetric containers.) Proceed with gas-liquid chromatographic analysis (see footnote 4).

Notes on DDT/PCB Separation Procedure

1) Elution with hexane instead of pentane during the silica gel chromatography fails to provide the necessary separation of DDT from PCB. Hexane is reported to contain variable amounts of benzene, which would obviously affect an already delicate separation. Use of UV-quality pentane or hexane has been recommended by others, and might allow use of hexane in warm weather.

2) For high residue level samples, evaporation of the Florisil eluate to ca. 1 ml is not necessary; instead an appropriate aliquot is used. However, no more than 1 ml of the eluate should be placed on the silica gel column because the hexane may contain benzene.

Procedure Variations

Plankton and Other High-Moisture Samples

Plankton do not homogenize well using the standard procedure. They also contain water in excess of the amount that 20 ml of 1:1 IPA/benzene can absorb. Addition of Na_2SO_4 before homogenization overcomes both difficulties. Na_2SO_4 not only absorbs water, but also serves as a grinding aid.

To the weighed sample of plankton add 25 ml of 1:1 IPA/benzene; then add 25 ml hexane and 10-15 g Na_2SO_4. Homogenize 5 min and proceed as usual.

During the 45-min boildown, scrape the material on the bottom of the flask. Pile up the solids to leave areas of the flask bottom in direct contact with the solvent to improve boiling action and prevent bumping. Cool. If water separates, add Na_2SO_4.

Filter through glass wool and proceed as usual (step 6 under Extraction).

In order to compensate for the low residue level usually found in plankton, place 2 ml of the extract on the Florisil column for cleanup.

Fishmeals or Dry Feeds

If the standard extraction procedure is used for meals and animal feeds, the finely ground meal forms a layer on the bottom of the Virtis flask which causes bumping and loss of solvent during the 45-min boildown. Extraction with hexane provides as good recovery as IPA/benzene. This substitution allows omission of the boildown.

1) Homogenize sample with 20 ml of hexane. Wash down Virtis blades and Teflon top with minimal amount of hexane. Add 10 g Na_2SO_4.

2) Immediately filter through glass wool tightly wadded to remove as much of the solids as possible. Wash flask and funnel with a minimal amount of hexane so that the volume of the centrifuge tube is not exceeded (35-40 ml).

3) Stir to mix and centrifuge at 1,500 rpm for 45-60 min at 10°C. (There should be about 35 ml of clear solution with less than 1 ml of solids.)

4) Record volume, subtracting 50% of the volume occupied by the solids. (Although this involves an approximation, the error involved should be no more than 2%.)

5) Decant the supernatant liquid into a storage bottle containing 1 g Na_2SO_4. Proceed with Florisil cleanup (step 9 under Cleanup).

Fish Oil

Homogenization and extraction of oil are unnecessary.

1) On an analytical balance weigh accurately about 2 g of oil into a 50-ml graduated centrifuge tube.

2) Dilute to about 20 ml with hexane and swirl to dissolve the oil completely.

3) Record the volume.

4) Place in a storage bottle, containing 1 g Na_2SO_4, and proceed with the usual cleanup (step 9 under Cleanup).

NOTE: For greater accuracy in oil analysis, weigh accurately about 2.0-2.5 g oil into a 25-ml volumetric flask. Dilute to volume with hexane. Shake thoroughly. Place sample in storage bottle and proceed at step 9 under Cleanup.

Paper

This procedure is included because occasionally fishery samples come in contact with contaminated packaging and labelling materials, such as carbonless carbon paper and cardboard. Although the procedure has not been validated by collaborative studies, it provides guidelines for an analysis relevant to fishery studies.

Cut the paper (or cardboard) into small pieces, approximately 1 cm on a side, with a scissors or office paper cutter, which has been cleaned thoroughly with iso-octane or hexane. Mix the paper thoroughly and weigh ca. 7 g into a Virtis flask. Add 15 ml distilled water and mix thoroughly with the paper. Allow the mixture to stand 2-5 min, stir again, and dilute with portions of 1:1 IPA/benzene to a total of 70 ml. Homogenize the mixture briefly at low speed. Push the paper down with the Virtis blades, then homogenize briefly. Repeat the process until the paper is completely homogeneous, approximately 10 min total homogenization time. Follow the usual boildown and Florisil procedures.

Procedure For Dieldrin and Endrin

Saponification[6] and Extraction

1) Weigh 10 g of material to be analyzed into a 250-ml Erlenmeyer flask. For oil, use only 2 g.

2) Dissolve 10 g of KOH in 6 ml distilled water. Slowly dilute with 34 ml of ethyl alcohol (95 or 100%). Swirl until clear.

3) Pour the alcoholic KOH over the sample and heat in a water bath without boiling for 20 min; the exact temperature is not critical.

4) Allow the mixture to cool. Pour the liquid portion into a 250-ml separatory funnel and rinse out the Erlenmeyer flask with 50 ml of water, divided into 4 or 5 portions. Avoid pouring any solids into the separatory funnel. For finely powdered samples like meal, filter the sample through a wad of glass wool and rinse the glass wool carefully with each rinse.

5) Add 15 ml hexane to the separatory funnel and shake for 2 min. Open the stopcock several times during shaking to relieve the pressure buildup. Allow the layers to separate completely, usually about 30 min.

6) Drain off the aqueous layer into the Erlenmeyer flask from which it came. Pour the hexane layer into a 30-ml beaker. Do not let any water escape into the beaker. Cover the beaker tightly with aluminum foil.

7) Pour the aqueous layer back into the separatory funnel and repeat step 5.

8) Drain off the aqueous layer and discard it.

9) Return the hexane extract in the beaker to the separatory funnel. Rinse the sides of the beaker with 1 ml hexane. Add the hexane wash to the extract in the separatory funnel.

10) Wash the hexane extract with 10 ml water by rotating the separatory funnel gently to avoid emulsion formation. *Do not shake.* Allow the layers to separate and discard the aqueous layer.

11) Pour the hexane layer into a 50-ml graduated cylinder. Do not transfer any water to the cylinder. Record the volume. Pour the extract into a 23-ml borosilicate screw-cap bottle (with Teflon-lined cap) containing 1 g Na_2SO_4.

Cleanup

12) Prepare a Florisil column by filling a 9 mm i.d. × 150 mm glass tube, plugged with glass wool, with ca. 4 cm of Florisil. Or use a 7 mm i.d. × 150 mm tube containing ca. 5 cm of Florisil. (The longer column of adsorbent may give slightly better cleanup.) Wet the Florisil with benzene and wash it with 4 to 5 ml benzene added 1 ml at a time. Wash it next with 10 ml hexane (or more) added 1 ml at a time. Pipette 2 ml of the hexane extract onto the column. Put a 12-ml graduated centrifuge tube under the column. Elute with hexane added 1 ml at a time. Collect the first 12 ml of hexane eluate, which contains DDMU (the dehydrochlorination product of TDE), DDE, and PCB. (They may be quantitated if desired.)

Place a second 12-ml centrifuge tube under the column. Change eluant to benzene; add it 1 ml at a time. Collect the first 10 ml of eluate. Place a modified micro Snyder column on the centrifuge tube to prevent loss of residues during evaporation. Concentrate the eluate containing dieldrin and endrin to an appropriate volume (1-3 ml) for

[6]Saponification in the presence of some proteinaceous materials has been reported to cause degradation of dieldrin. As stated above, recovery studies are always important.

gas-liquid chromatographic analysis (see footnote 4).

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GROWTH OF JUVENILE SPOT PRAWN, *PANDALUS PLATYCEROS*, IN THE LABORATORY AND IN NET PENS USING DIFFERENT DIETS

Floating net pens have been used to culture Pacific salmon, genus *Oncorhynchus*, in the marine waters of the West Coast since 1969 (Mahnken 1975). Although it has been a monoculture effort to date, use of a companion crop species such as the spot prawn, *Pandalus platyceros* Brandt, could diversify and enhance this industry.

In 1975 the National Marine Fisheries Service selected the spot prawn to examine as a potential companion species to net pen-reared salmon. The spot prawn was selected as a candidate for several reasons: 1) it has a rapid growth rate and large size compared with other pandalids (Butler 1964); 2) it can be successfully cultured to maturity in captivity (Prentice 1975); 3) it will reproduce in captivity, often for two consecutive years (Rensel and Prentice 1977); 4) it is gregarious and is normally not cannibalistic; 5) it adapts to vertical or horizontal substrates; and 6) it scavenges for, and accepts, a wide variety of foods (Wickins 1972).

Coincident to investigating the prawn as a companion crop to salmon, several prawn diets were evaluated with prawns held in tanks and net pens at the NMFS Aquaculture Experiment Station on Puget Sound near Manchester, Wash. These experiments were conducted using diets made up of underutilized marine species or fishery byproducts that are available to most salmon farmers.

Materials and Methods

The spot prawns used in the experiments were laboratory-reared progeny of females captured in Hood Canal, Wash. Three concurrent experiments with juvenile prawns (<1 yr of age) began 10 July 1975 (Table 1).

Experiment A was conducted in the laboratory where prawns were held in flowing seawater tanks at 110 animals/m^2 of immersed substrate. Four diets were evaluated: 1) steamed mussel, *Mytilus edulis*, meat; 2) chopped salmon that had died in nearby net pens; 3) feces and pseudofeces from the Pacific oyster, *Crassostrea gigas* (eight oysters per replicate having a mean weight (total) of 153 g); and 4) no food (control). Diets 1 and 2 were fed every other day while diet 3 was always present in varying amounts. A sample of 10 prawns for each of four replicates was measured during each of

TABLE 1.—Growth and survival of juvenile *Pandalus platyceros* during three tests.

Experiment	Location	Diet	No. of replicates	Start of experiment: No. of prawns in each replicate	Start of experiment: Mean weight (g)	60 days after start of experiment: Mean survival (%)	60 days after start of experiment: Mean weight (g)	End of experiment: No. of days	End of experiment: Mean survival (%)	End of experiment: Mean weight (g)
A (prawns alone)	Laboratory tanks	Mussel	4	25	0.72	82	2.52	90	74	3.14
		Salmon	4	25	0.62	83	2.27	90	71	2.61
		Oyster wastes	4	25	0.69	64	1.06	(1)	(1)	(1)
		No food	4	25	0.64	26	1.07	(1)	(1)	(1)
B (prawns alone)	Net pens	Mussel	2	200	0.64	98	3.14	365	69	10.30
		Salmon[2]	2	200	0.63	98	2.79	365	64	10.61
C (prawns and salmon)	Net pens	Variety of feeds[3]	1	100	0.64	93	3.42	206	93	8.60

[1]Terminated at 60 days.
[2]Includes net-fouling organisms.
[3]Includes salmon mortalities, uneaten fish feed (Oregon moist pellets), salmon feces, and net-fouling organisms.

three 30-day sampling periods. Carapace lengths[1] and individual wet weights (nonblotted) were measured to the nearest 0.5 mm and 0.01 g, respectively. In all experiments growth data were analyzed by one-way analysis of variance and survival by chi-square tests.

In Experiment B, prawns were held in two net pens measuring 1.2 × 1.8 × 1.8 m and constructed of knotless nylon web (6.8-mm stretched measure mesh). Each pen was vertically divided into three equal compartments (6.5 m^2 of substrate each) with only the outer two being stocked with prawns. The prawns were stocked at a density of 30.8/m^2 of immersed substrate. The net pens were covered with black plastic to prevent bird predation and to reduce light intensity. Two dietary treatments were evaluated, mussel meat and salmon. Each treatment consisted of two replicates and was fed exclusively on one of the two diets. Feed was to excess every other day.

A sample of 50 prawns/replicate (100/treatment) was measured for length and weighed during each of eight sampling periods, except during the last three periods in which all survivors were measured and weighed. The prawns were sampled at the beginning of the experiment and 32, 60, 88, 146, 205, 292, and 365 days later.

In Experiment B, in addition to evaluating the diets, we studied the net cleaning ability of the prawns and the value of the organisms on the net (i.e., the net fouling organisms) as a supplementary food source. Samples of net fouling organisms were taken from inside and outside of a compartment containing prawns (test) and inside and outside of one not containing prawns (control). The nets were selected at random, and each sample consisted of all the organisms on the net within the area of two 20-cm-diameter circles; one circle was at 0.25-m depth, and the other was at 1.0-m depth. The material collected was identified, enumerated, and measured volumetrically. The nets were sampled during November 1975 and March 1976.

In Experiment C, juvenile prawns were stocked in a net pen with coho salmon, *Oncorhynchus kisutch*, (age-group 0) that averaged 20 g each. A single net pen (without dividers) having a substrate area of 10.8 m^2 was used. Prawn density was 9.3/m^2 of substrate, and salmon density was 82/m^3 of water. The salmon were fed Oregon moist pellets at 3% body weight/day; however, no feed was provided for the prawns other than what they could scavenge. All the prawns were measured at each of seven periods: at the beginning of the experiment and 15, 33, 60, 89, 146, and 206 days later.

Care was taken to standardize culture conditions such as lighting, substrate type, and water temperature within each experiment. This was not practical between experiments because of inherent differences between laboratory and net pen work.

Stocking density differed between experiments, but its impact on growth and survival (agnostic behavior and feeding dominance) was minimized by distributing an excess of food throughout the rearing enclosure. In several years of behavioral observations we have rarely seen overtly agressive or cannibalistic behavior in spot prawns.

Results and Discussion

Mussel-fed juvenile prawns had the best survival and growth rate of all the prawns raised in the laboratory tanks (Experiment A); 74% of the

[1]Carapace length is defined as the distance from the base of the eyestalk to the posterior middorsal edge of the carapace.

prawns survived, and they had a final mean weight of 3.14 g (Table 1). The prawns fed salmon were significantly smaller ($P<0.01$) than the mussel-fed group. However, the growth of prawns in both the mussel and salmon diet groups equaled or exceeded the growth reported for a natural population in British Columbia (Butler 1964).

Growth was similar between oyster waste and no food diet groups (Table 1), but survival was significantly different ($P<0.01$), 64% for oyster waste and 26% for no food supplement. Prawns fed oyster wastes or receiving no food grew at a slower rate than the prawns in the other two diet groups; this portion of the study was terminated after 60 days.

The poor growth of prawns fed oyster wastes contrasts with the good growth of lobster *Homarus americanus* fed algae and oyster wastes in a sewage enriched raceway system (Mitchell 1975). In that study intermediate organisms that fed on the solid wastes of oysters were also available as a food source for juvenile lobsters. In our study, raw unfiltered seawater was used, but cleaning the tanks twice weekly prohibited the establishment of intermediate organisms.

Prawns in the net pens (Experiment B) grew significantly faster than those in the laboratory (Experiment A) for both mussel- ($P<0.01$) and salmon-fed ($P>0.01$) treatments (Table 1). Further, there was no significant difference in the growth ($P>0.10$) or survival ($P>0.25$) of prawns fed mussel or salmon in the pens as there had been in the laboratory tanks.

In the net pens, the presence of net fouling organisms as an additional food source for the prawns could explain the improved growth over that seen with the same basic diets used in the laboratory. Net fouling organisms could have provided nutritional requirements that were deficient in the basic diets as provided in the laboratory.

Prawns in both diet groups were observed removing organisms that were on both the inside and outside surfaces of the net pens using their second periopods. The amount of net fouling organisms was reduced by the prawns in these en-

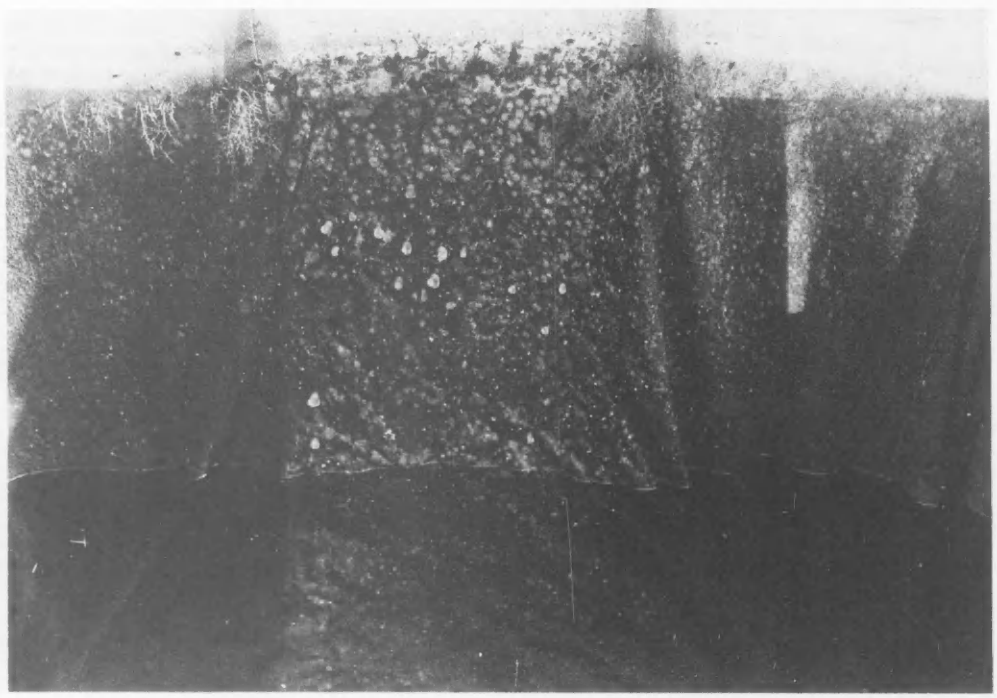

FIGURE 1.—Webbing of a three-chambered net pen showed reduced fouling in the right and left chambers (spot prawns present) compared with the center chamber without prawns.

closures (Figure 1, Table 2). The largest amount of organisms occurred at the shallower depths of the nets as in Moring and Moring's (1975) study of salmon net pens at the same site. Mussels, ascidians, and tubicolous polychaetes, *Spirorbis* sp., contributed the most fouling in the control chambers (without prawns). Except for a few *Spirorbis* sp., the net pen chambers with spot prawns were completely clean. Little algal growth was present due to the reduction of light by the black plastic covers.

Rearing prawns and salmon in the same net pen (Experiment C) proved encouraging. After 6½ mo of culture the growth of these prawns (Figure 2) exceeded that of the monoculture Experiment B ($P<0.01$) and that reported for a natural population (Butler 1964). Survival was 93% and not significantly different ($P>0.95$) from that of Experiment B.

There was no evidence of adverse salmon/prawn interaction. The types of food available to the prawns when reared with salmon included: dead fish, uneaten fishfood pellets, fish feces, and net-fouling organisms. The relative contribution of each was unknown.

A limiting factor to stocking juvenile prawns in commercial salmon net pens is the requirement that the prawns must be large enough to prevent them from going through meshes of the net. Smaller "nursery" nets of reduced mesh size could be hung inside the main salmon nets until the prawns reach a suitable size (about 4 g, or 3 mo of age).

Several advantages might accrue from using a scavenger, such as the spot prawn, as a companion crop in salmon culture. In Experiment B a reduction in net fouling was seen in net pens with prawns (Table 2, Figure 1). This reduction will aid salmon culture because it would allow greater water circulation within the enclosure, thus increasing dissolved oxygen levels and flushing of

TABLE 2.—Displacement volumes (milliliters) of fouling organisms on the inside and outside surfaces of net pens with and without *Pandalus platyceros* from July 1975 to March 1976. All pen chambers were clean at the start of the experiment. Sample area was 314.2 cm² of vertical mesh.

Location of sample	Depth of sample (m)	Net pen compartment with prawns		Net pen compartment without prawns	
		Nov. 1975	Mar. 1976	Nov. 1975	Mar. 1976
Inside of net	0.25	0.40	0.00	26.40	41.55
	1.00	0.00	0.00	10.50	12.03
Outside of net	0.25	0.25	0.50	9.00	17.00
	1.00	0.10	0.40	6.00	11.53

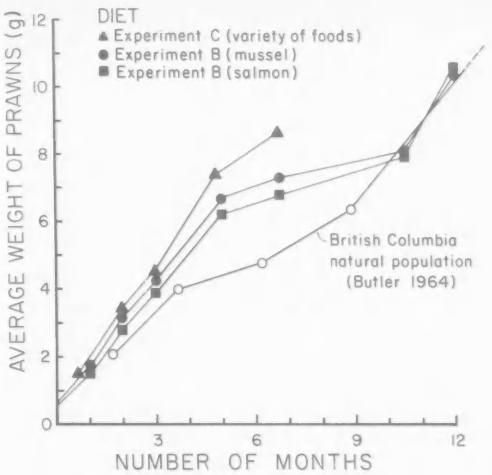

FIGURE 2.—Growth of juvenile *Pandalus platyceros* in net pens compared with a natural population.

metabolic wastes from the pens. A reduction in net maintenance cost might also be realized. Experiments B and C demonstrated that fish in the presence of net-fouling organisms was an acceptable food for the prawn (Figure 2); the utilization of dead salmon by a scavenger would be a valuable conversion of an otherwise unused protein and would reduce the labor needed to remove salmon mortalities from the system.

Further experiments are needed to determine proper stocking densities of prawns and salmon to maximize growth rates, survival, and to make optimum use of the net cleaning activities of the prawns. Further, while our studies showed that a single diet fed to prawns in the laboratory was not adequate for rapid growth, other studies (Kelly et al. 1976) have shown that combination raw diets could produce adequate growth. These combination diets need to be evaluated in the net pen system.

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LARVAL LENGTH-WEIGHT RELATIONS FOR SEVEN SPECIES OF NORTHWEST ATLANTIC FISHES REARED IN THE LABORATORY

Growth is an important connecting link in the functional influence of biotic and abiotic factors on the dynamics of fish populations. Length-weight relations are used by fishery scientists to describe the growth characteristics of species or populations and as a basis of evaluating the consequences of environmental influences on growth. Length-weight relations are also used in assessing production when combined with age and growth information and in determining length or weight in a situation where either one or the other is unknown due to sampling procedures.

Studies of the early life of fishes are receiving increasing emphasis, particularly with regard to growth and survival in the larval stage. Survival during this period is thought to be minimal and potentially variable from year to year. Small changes of tenths of a percent in mortality have the potential to produce orders of magnitude differences in eventual adult populations. Larval growth can be influenced due to food limitations and varying abiotic factors (Houde 1974; Lasker 1975; Laurence 1977). Because of these facts, fishery scientists are particularly concerned with two aspects: 1) quantifying variable larval growth and survival, relating it to subsequent year-class recruitment, and applying it to traditional stock-recruitment relationships where recruitment has often been considered constant; and 2) the potential use of this type of information in evaluating the increasing effects of pollution or other environmental perturbations because of the fragility and sensitivity of larvae to changing or altered environmental variables.

Solutions to these problem areas require quantitative knowledge of growth parameters of larval fishes, and length-weight relations can be helpful in providing information or establishing relationships between pertinent sets of data. It is generally thought that weight[1] is a better measure of absolute growth of fish larvae than length as well as the prime determinant of condition when combined with length. Many species exhibit allometric or disproportionate length-weight growth. This is especially true during the period of metamorphosis when some species display varying or unusual body proportions with age (Blaxter 1969) and length does not increase in proportion to increasing weight. Additionally, recent attempts to construct models of larval survival, as influenced by environmental variables and density dependent feeding relationships, require weight determinations for estimates of biomass and caloric turnover between larval and prey trophic levels.

There is an extensive data base to asses larval fish growth and survival based on ichthyoplankton collected on survey cruises during the last 75 yr by marine laboratories throughout the world. Unfortunately, almost all of these data are in standard or total length measurements as they are much more easily and rapidly taken than dry weights. The difficulty involved in obtaining dry

[1]Weight for species in this research refers to dry weight. Dry weight is the most accurate for fish larvae because accurate wet weights are difficult to obtain and yield variable results on organisms as small as fish larvae.

weights of young stages has been overcome to a certain degree with the advent of experimental laboratory programs at a few research facilities during the last 10 yr.

The experimental larval fish program at the Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, has been studying growth, metabolic, and trophodynamic factors for a number of important commercial and sport species, and it is the object of this report to present larval length-weight relations for seven species including Atlantic cod, *Gadus morhua*; haddock, *Melanogrammus aeglefinus*; scup, *Stenotomus chrysops*; Atlantic herring, *Clupea harengus*; winter flounder, *Pseudopleuronectes americanus*; summer flounder, *Paralichthys dentatus*; and yellowtail flounder, *Limanda ferruginea*. The larval length-weight relations presented here are previously unreported in the literature for six of the seven species with the exception of the Atlantic herring, which is included because it represents the only data available for western North Atlantic stocks.

Materials and Methods

All larvae were obtained from experimental spawning of adults in the laboratory and reared by techniques reported by Smigielski (1975a, b) and Laurence (1975). The length-weight data were collected coincident with a variety of experimental studies on larval growth, survival, metabolism, and feeding reported by Laurence (1974, 1977, 1978, and as yet unpublished).

In all cases the data were collected from larvae reared at prey concentrations in the range of 0.5 to 3.0 organisms/ml. Concentrations of 0.5 and above have been shown to be adequate for normal growth in the studies cited above. Rearing temperatures were optimum for growth and survival or within a 3°C nonlethal range about the optimum depending upon the experiment from which the data were taken. Optimum temperatures determined in laboratory studies for rearing the seven species were 7°C for cod and haddock, 8°C for winter flounder, 10°C for herring and yellowtail flounder, 16°C for summer flounder, and 18°C for scup.

Length measurements were taken from the tip of the snout to the end of the notochord in the preflexion stage. During flexion of the notochord measurements were taken to a line vertically perpendicular to the tip of the notochord until the hypural bones became prominent or exceeded the line vertically perpendicular to the notochord tip. At this time, a standard length measurement to the posterior end of the hypural plate was recorded. Since the original experiments were not designed for developmental anatomy purposes, the different flexion stages were not recorded coincident with the length and weights.

Lengths were recorded to the nearest 0.1 mm with a filar ocular micrometer. Dry weights were determined after rinsing larvae in distilled water, pipeting onto a glass Petri dish, and drying to a constant weight at 60°-90°C for 24 h. Individual dry weights were recorded to the nearest 0.1 μg on a gram electrobalance.

All measurements were made on post yolk-sac larvae that were freshly sacrificed and unpreserved. The data points for each species represent lengths and weights for individual larvae except for winter flounder and haddock. The data for these two species are the means of lengths and weights for samples of 10-25 larvae collected on a weekly basis during different experiments. The experimental procedures precluded the matching of individual lengths with weights for these two species.

Regression equations and associated parameters were calculated as geometric mean, functional regressions using log base 10 transformed data according to the methods of Ricker (1973) rather than using the previously standard predictive, regression techniques. Ricker demonstrated the advantages of using functional rather than predictive regression calculations to reduce bias in length-weight conversions where the populations of measurements are typically open ended, where only a portion of the length and weight distributions are represented, and where the variability may be more inherent in the biological material itself rather than the means of measuring length and weight.

Results and Discussion

The exponential relation between length and weight for all seven species are presented in linearized form by logarithmic transformation in Figures 1-7. The larvae studied in this research are from different taxonomic families (Clupeidae, Gadidae, Sparidae, Bothidae, and Pleuronectidae), represent different adult life styles (pelagic and demersal), develop in a range of different temperatures, and demonstrate different patterns of metamorphosis from larval to juvenile stages.

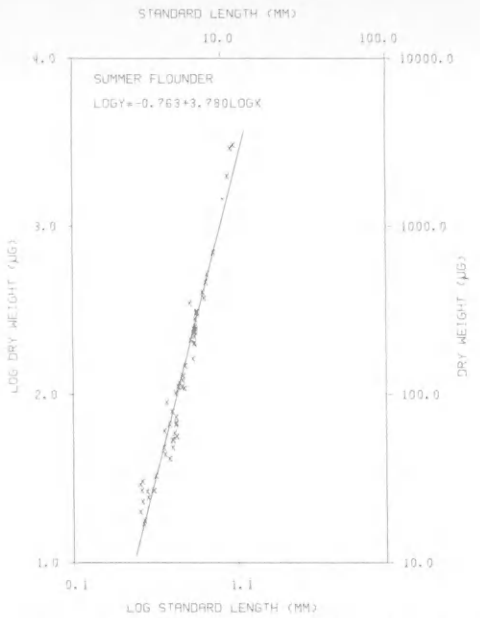

FIGURE 1.—Standard length-dry weight relationship of larval summer flounder.

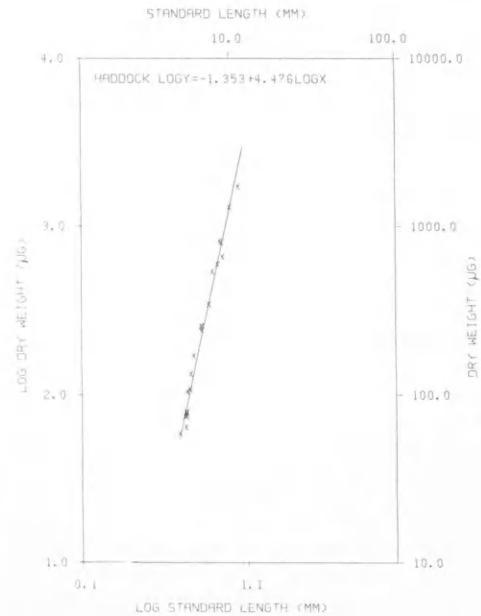

FIGURE 2.—Standard length-dry weight relationship of larval haddock. Points represent means for length and weight of samples of 10-25 larvae.

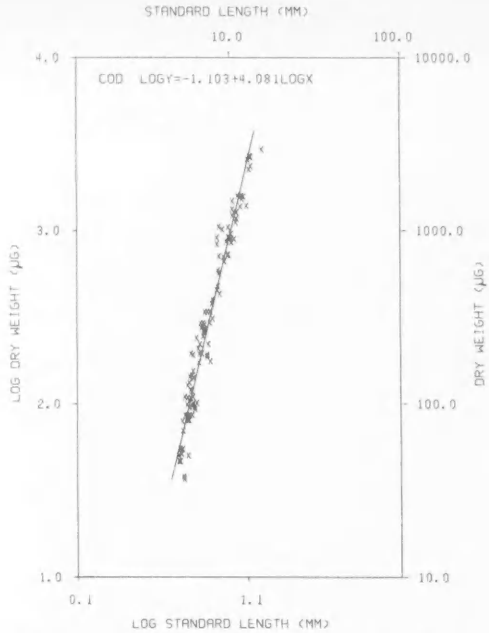

FIGURE 3.—Standard length-dry weight relationship of larval cod.

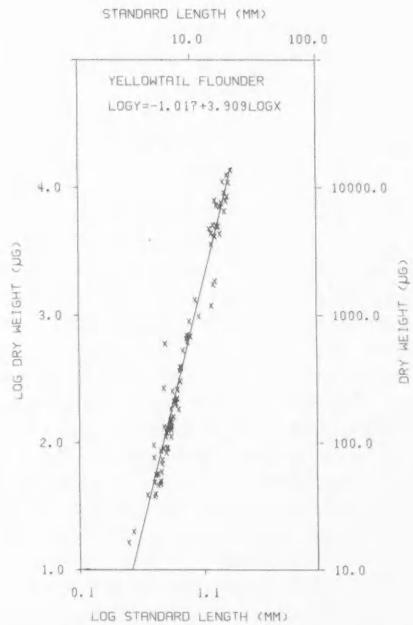

FIGURE 4.—Standard length-dry weight relationship of larval yellowtail flounder.

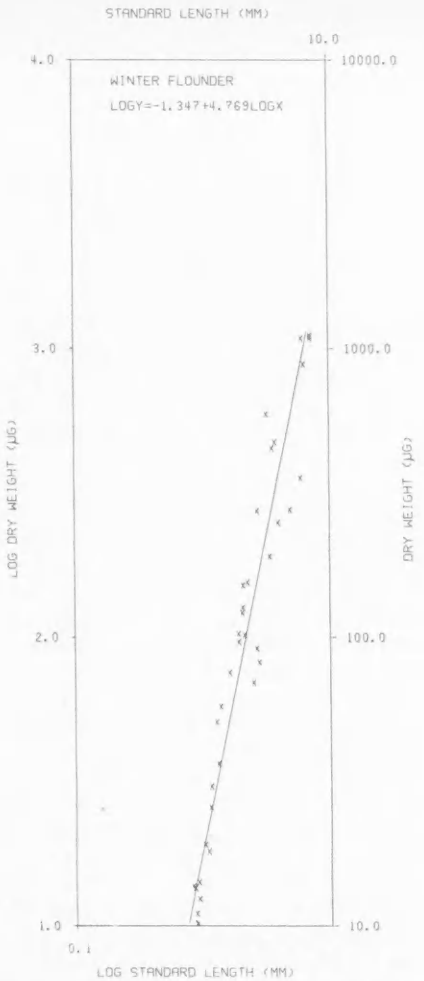

FIGURE 5.—Standard length-dry weight relationship of larval winter flounder. Points represent means for length and weight of samples of 10-25 larvae.

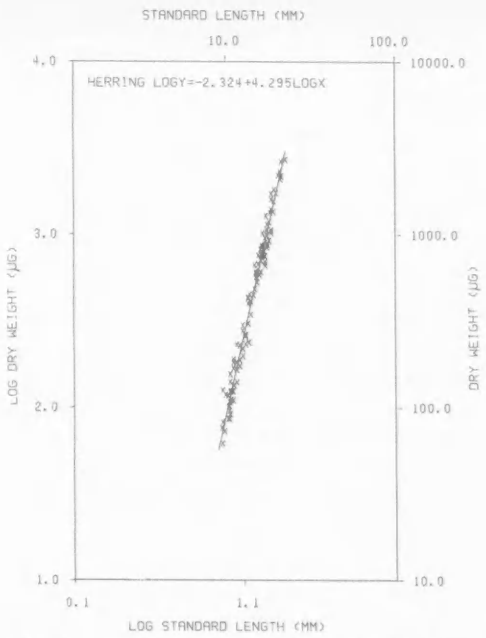

FIGURE 6.—Standard length-dry weight relationship of larval Atlantic herring.

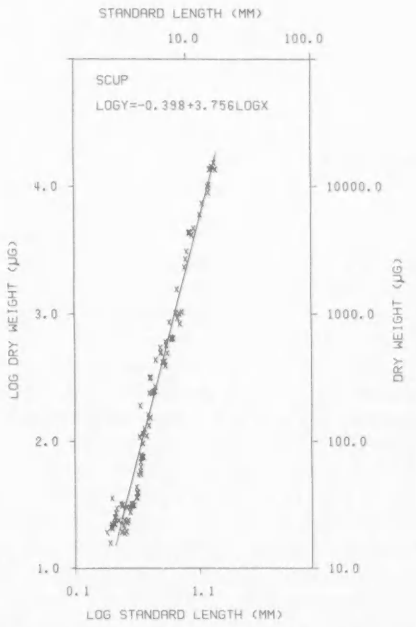

FIGURE 7.—Standard length-dry weight relationship of larval scup.

In spite of these differences, a visual examination of the length-weight regression equation coefficients and associated parameters for all species reveals no obvious correlations with the differences (Table 1). It would not be prudent to statistically test for differences or associations between the species because data for haddock and winter flounder were averaged. Ricker (1973) cautions that averaging changes the variances associated with the variables, particularly the independent variable, so that a comparison between

TABLE 1.—Regression parameters for length-weight relations of seven species of laboratory-reared larval northwest Atlantic fishes.

Larval species	Number sampled	Correlation coefficient	Coefficient of determination	Regression coefficient	Standard error of regression coefficient	95% C.I. about regression coefficient
Summer flounder	57	0.997	0.994	3.780	0.039	3.702-3.858
Yellowtail flounder	80	0.995	0.990	3.909	0.044	3.821-3.953
Herring	98	0.997	0.993	4.295	0.037	4.221-4.369
Scup	100	0.997	0.993	3.756	0.028	3.692-3.820
Cod	104	0.997	0.995	4.081	0.029	4.023-4.104
Haddock[1]	23	0.997	0.995	4.476	0.071	4.328-4.624
Winter flounder[1]	36	0.991	0.982	4.769	0.110	4.545-4.993

[1]Data represent means for length and weight of samples of 10-25 larvae.

averaged and unaveraged data is not valid: although he does not discredit the use of averaged data by itself. Also, seven species, some of which are closely related taxonomically, probably do not constitute enough cases for drawing conclusions about functional differences. Consequently, these length-weight relations should properly be considered individually as empirically derived relations for each particular species.

The length-weight relation of fishes usually approximates the cube law relationship in which the weight is proportional to the cube of the length (Beckman 1948; Rounsefell and Everhart 1953). This is usually true for adult fishes; however, results of this research imply that it is not necessarily so for larvae. All the length exponents for the species investigated in these studies were >3.6 with a mean value of 4.152. It would seem then that the dry weight of larval fishes may be more closely proportional to length to the fourth power rather than cubed. Length-weight relations for fish larvae are scarce in the literature. Examination of the data available ($\log_{10}$ formulation) seems to substantiate that the length exponent is always greater than three and more closely approximates four. Marshall et al. (1937) presented a total length-dry weight equation for larval herring, the only species with data available to compare with this study, equivalent to $\log W = -5.6990 + 4.52 \log L$. The length exponent is >4 and similar to the value of 4.295 for herring in this research. Ehrlich et al. (1976) also presented a similar standard length-dry weight relation for Firth of Clyde herring larvae ($\log W = -5.7052 + 4.5710 \log L$) as well as a relationship of $\log W = -4.3043 + 3.9155 \log L$ for larvae of plaice, *Pleuronectes platessa*. Stepien (1976) reported a standard length-dry weight relationship for larval sea bream, *Archosargus rhomboidalis*, of $\log W = -0.5144 + 4.2816 \log L$, and Lasker et al. (1970) reported a standard length-dry weight relationship for northern anchovy larvae, *Engraulis mordax*, of $\log W = -3.8205 + 3.3237 \log L$.

It is acknowledged that variables such as temperature and feeding conditions can influence growth and complicate length-weight relations. These factors may have contributed to some variability in the present study. However, it is felt that these influences were minimized by the experimental feeding levels and temperatures which were within ranges for adequate growth and survival, and any changes in length or weight were most likely mitigated together causing little effect on the form of the length-weight relation. This is supported in studies of haddock larvae (Laurence 1974) where condition factors were similar and randomly associated with prey concentrations >0.5 organisms/ml.

The use of larval length-weight relations for extrapolation may result in some underestimation or overestimation at the smallest and/or largest sizes due to changes in growth rates for yolk-sac or metamorphosing larvae. Farris (1959) suggested that growth rates of larval marine fishes could be separated into three different phases; the first two prior to yolk absorption and the third following. Zweifel and Lasker (1976) presented a mathematical interpretation of larval growth with age defined by the Laird-Gompertz growth function. They noticed two growth cycles; one extending from hatching to yolk absorption and the other following yolk absorption. This variability in the small sizes is probably not inherent in the data of this study because larvae were not included until yolk was absorbed and active feeding had commenced. Some variability may be present in the upper range of sizes in these length-weight relations. In some cases data for larger larvae are not as extensive as for smaller larvae. Also, the majority of the largest individuals for each species were either undergoing or had completed metamorphosis where changes in growth rates of length or

weight might cause allometry. Zweifel and Lasker (1976) briefly considered the length-weight relation in terms of a modified Gompertz-type relation and noted overestimation problems in extrapolation at the largest sizes.

Length-weight relations have merit, but their usefulness is greatly enhanced when combined with other studies, particularly those on age. Length-weight by itself does not necessarily imply rate of change because of the potential influence the environment may have on changing growth with time. However, when correlated with age and compensated for change in rate due to biotic and abiotic influences, length-weight studies can be an important component in estimating growth, survival, and population production.

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EFFECT OF THERMAL INCREASES OF SHORT DURATION ON SURVIVAL OF *EUPHAUSIA PACIFICA*

Euphausiids are an important source of food for many valuable species of fish including herring, cod, pollock, and salmon. Cooney (1971) reported that *Euphausia pacifica* was the most abundant species associated with the diffuse scattering layer at all locations in Puget Sound, Wash. He found that during the day euphausiids are most abundant between depths of 50 and 100 m and that at night most of the population migrates into the upper 50 m. Cooney's findings indicate that great numbers of euphausiids could be drawn through

the condenser cooling systems of thermal nuclear power plants where they would encounter a sizable thermal shock.

Zooplankton entrained in a power plant cooling system located in a saltwater environment could be subjected to an average temperature increase ranging from 12° to 16°C (Coutant 1970). In some plants, the increases are as high as 19°C. Maximum temperatures would be reached in <1 min in the condenser and would be maintained for at least 9 min in a diffuser discharge system and at almost maximum temperature, for possibly up to 21 min, in a discharge canal system. Other factors that could cause damage to euphausiids in a cooling system include pressure changes, abrasion, and toxic substances.

I simulated the thermal conditions encountered in a cooling system to determine the temperature increases that *E. pacifica* could resist for short periods (15 and 30 min). This information can be applied to the design and operation of cooling systems to protect zooplankton.

These studies were conducted at the National Marine Fisheries Service's Mukilteo Field Station, Washington, during 1971-74.

Methods

Euphausiids for these experiments were captured during daylight hours in Port Gardner of northern Puget Sound, Washington, between Mukilteo and Gedney Island. A 10-m net with 333-μm aperture Nytex[1] netting was towed at a depth of about 60 m at a rate of 4.6 km/h. Tows were usually of a 5-min duration. A 946-ml glass bottle was used as a collection receptacle to protect the animals.

As soon as the net was retrieved, the catch (consisting mostly of euphausiids) was divided between two or three 18.9-l Nalgene carboys filled with fresh seawater and covered with black polyethylene sheeting to exclude light. The catch was taken immediately to the laboratory, usually <2 km away, where the euphausiids were separated from other organisms in the catch and placed in 5-l battery jars (23 × 14 × 17 cm) of fresh seawater. They were then placed in a dark, low-temperature incubator set at their previous ambient seawater temperature where they were held before and after testing.

The test apparatus consisted of a series of 5-l battery jars filled with seawater that were maintained at specific temperatures by immersion heaters activated by temperature controllers (Craddock 1976). The jars were in a primary bath of running seawater at ambient temperature and air was continuously bubbled into the jars to eliminate stratification.

Test containers for holding the euphausiids were polyvinyl chloride boxes of 5 cm^3 with two opposing sides having 4-cm diameter cutouts covered with 333-μm aperture Nytex netting to allow free water circulation. Styrofoam glued to the boxes provided flotation (Figure 1).

The temperature-time regime to which the euphausiids were subjected was designed to simulate their passage through a condenser cooling system. Coutant (1970) depicted a hypothetical temperature-time course for organisms entrained in condenser cooling water and discharged by diffuser or by discharge canal. An animal could be subjected to maximum temperature increases for up to about 10 min in a diffuser and up to about 20 min in a discharge canal system. Relative to his study, I chose 15- and 30-min exposure tests to represent the longest exposure that might be encountered. To simulate these conditions, test euphausiids were subjected to a given temperature ranging from 14° to 29°C for 15 or 30 min, starting from temperatures of 11° or 9°C. Euphausiids used as controls were always kept at the prevailing ambient temperature (approximately the same as the subsurface temperature of Puget Sound). Five 15-min tests were conducted during June-July 1971, four 30-min tests were run during June-August 1971, and two 15-min tests were made during March-April 1974.

The euphausiids were held 18 h or longer before testing to eliminate handling mortality and were then counted into test containers in seawater while the secondary baths were being raised to the test temperatures. Either 5 or 10 euphausiids were tested in each container, depending upon the numbers available for that particular test.

When all secondary baths became equilibrated at the test temperatures, the boxes containing the euphausiids along with a small amount of water were placed in the test baths. Water in the test containers was within 0.5°C of the test temperature in an average of 28 s after introduction. At the end of the exposure period, the test boxes containing the euphausiids were removed from seawater at the test temperature and placed in fresh seawa-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

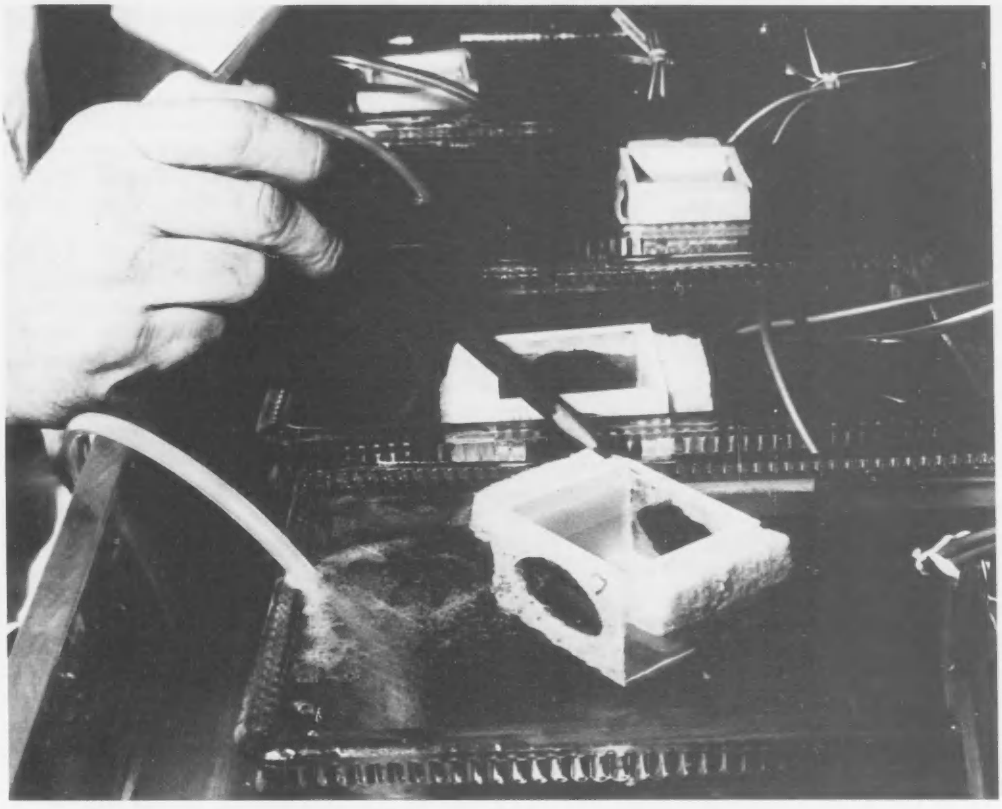

FIGURE 1.—Test chambers and apparatus for testing thermal effects on *Euphausia pacifica*.

ter at the acclimation temperature and maintained in the low temperature incubator. All lots were checked for mortality at 5, 10, and 15 min after introduction to the test temperature when the duration of the exposure was 15 min and also at 20 and 30 min after introduction for the 30-min exposure. All were again checked at 1, 24, and 48 h after testing. The 48 h survival was taken as diagnostic for the TL_{50}'s.

Temperature effects were evaluated on the basis of mortality during tests and 48 h after testing. Forty-eight hours was assumed to be a reasonable holding period to check for delayed mortalities—yet not long enough to cause mortality due to confinement and lack of food. A euphausiid was considered dead if no movement of the thoracic appendages, pleopods, or antennae could be detected using 3× magnification. I modified the term median tolerance limit (TL_{50}) to indicate the maximum 15- or 30-min exposure temperature survived by at least 50% of the experimental animals 48 h after testing. This should be considered the maximum temperature-time combination resisted.

Lengths of the test animals between the extreme tips of the rostrum and telson were taken at the end of each test. The mean-lengths of the euphausiids tested at the various seasons ranged from 12.11 to 18.37 mm (Table 1). The actual range was from 9 to 27 mm. Those tested in the early part of June were the largest; they exceeded those tested later in June by an average of 6.26

TABLE 1.—Sizes (millimeters) of *Euphausia pacifica* tested.

Dates	Mean	Range	Dates	Mean	Range
1971:			1974:		
June 2-9	18.37	14-26	Mar. 12	14.15	10-20
July 21-30	12.11	9-16	Apr. 12-16	13.85	10-23
Aug. 4-11	13.14	10-19			

mm. Those tested in August, March, and April had an average spread of only 1.01 mm.

Results

Controls in the different tests suffered no mortality during the exposure period except the June-July tests, where the 15-min group lost 7% of controls by the end of 48 h and the 30-min group lost 10% by the end of 48 h. The data were corrected to reflect the loss of the controls in the June-July tests, using the method of Tattersfield and Morris (1924) as reported by Sprague (1969).

Acclimation temperature influenced resistance. The TL_{50} of euphausiids given a 15-min exposure to elevated temperature was 25°C for those acclimated to 11°C; it was 23°C for those acclimated to 9°C. Exposure to 26°C resulted in survivals of 32% and exposure to 27°C resulted in almost immediate death (<15 min). In the 15 min 9°C acclimation test (March-April 1974), the TL_{50} was at 23°C and 47% were still surviving 48 h after exposure at 24°C. However, 15 min after exposure to 25°C, only 13% remained alive and all were dead in <15 min at 26°C. Figure 2 depicts the survival after a 15- and 30-min exposure to elevated temperatures and after a 48-h holding period.

Increasing the duration of exposure to test temperatures from 15 to 30 min when the ambient temperature was 11°C decreased the TL_{50} by 1° to 24°C. Of those tested at 25°C, only 44% survived 48 h after testing. At 26°C, only 2.5% survived the 30-min test period. None survived the test period at 27°C.

The logistic model was fitted to the data from the three different thermal shock tests. The probability of survival was taken to be the form P [survival at temperature x] $= 1/(1+e^{ax+b})$ where $e = 2.718$. This is the so-called logistic model and a and b are parameters which are estimated using the data. In the 15-min exposure of June-July 1971, $\hat{a} = 0.6544$ and $\hat{b} = -16.4138$; in the March-April 1974 exposure, $\hat{a} = 0.9568$ and $\hat{b} = -22.2860$; whereas in the 30-min exposure July-August 1971, $\hat{a} = 0.5173$ and $\hat{b} = -12.2572$. The estimates of TL_{50} and an approximate 95% confidence interval for it follow for the three tests: 1) 25.08°C, 24.51°-25.65°C; 2) 23.29°C, 22.76°-23.82°C; and 3) 23.69°C, 22.95°-24.44°C.

There was no obvious difference in the effect of a

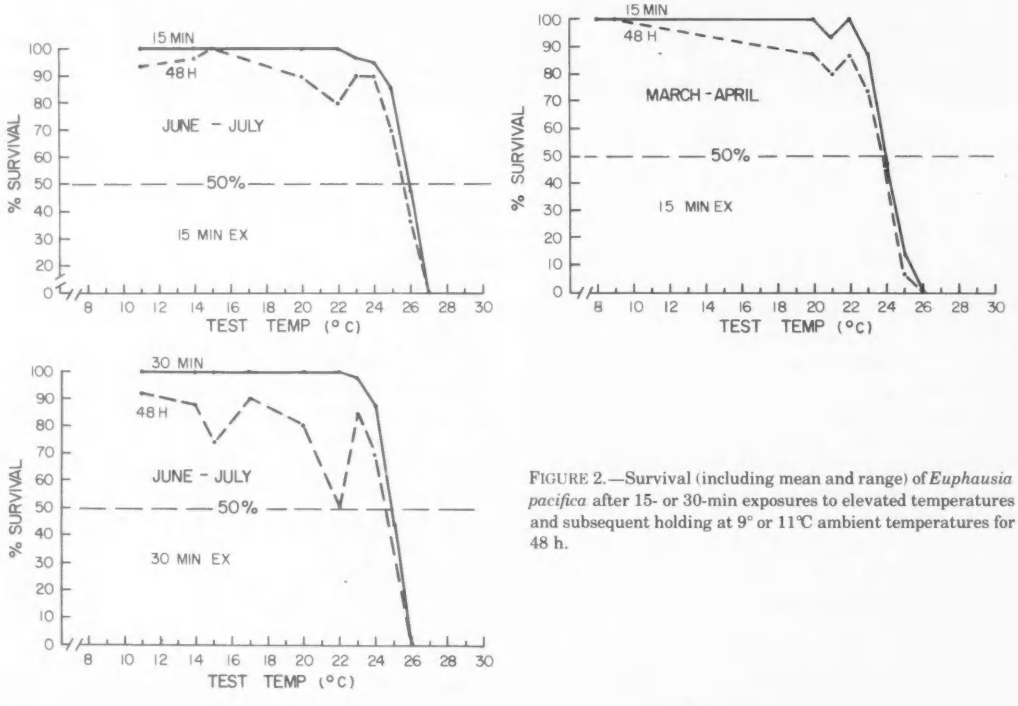

FIGURE 2.—Survival (including mean and range) of *Euphausia pacifica* after 15- or 30-min exposures to elevated temperatures and subsequent holding at 9° or 11°C ambient temperatures for 48 h.

short exposure to increased temperature on the largest or the smallest euphausiids tested. Two out of three groups tested for 15 min in early June (the largest euphausiids) exceeded 50% mortality after exposure to 26°C as did the two groups tested in late July (the smallest euphausiids).

Discussion

The intake of a condenser cooling system may entrain large quantities of euphausiids—depending to some extent on the depth of the intake, the season of the year, and even the time of the day. During the summer, fall, and winter, the young euphausiids make diurnal vertical migrations from the 50- to 100-m strata, rising daily to the surface during the dark hours. After sexual maturity in the early spring they descend even deeper until they inhabit depths over 200 m during their second winter. The following spring they rise to the surface for the second time to breed. The young euphausiids thus spend much of their first year at depths above 50 m, and older adults are again near the surface in the spring (Ponomareva 1963).

Gilfillan (1972) pointed out that *E. pacifica* is widely distributed and is abundant in water having differing temperature characteristics. His studies showed that *E. pacifica* from the Pacific Ocean were more easily stressed by changes in temperature and salinity than those from the west entrance of Strait of Juan de Fuca—which, in turn, were more readily stressed than those from Saanich Inlet. His results indicate that *E. pacifica* from inner Puget Sound would be among the most resistant to thermal stress of these different groups.

Temperatures encountered by euphausiids in Puget Sound normally vary only slightly from the surface to 100 m and deeper. From October through about May there is usually no change in temperature from the surface to 100 m, whereas in the summer the surface to 10 m or less may be a few degrees warmer (Lincoln and Collias[2]).

Seasonal temperature variations in most of Puget Sound are also small, ranging from a low of 7° or 8°C in February to 11°C in late July, August, and September. Even considering their vertical migrations in summer, euphausiids are normally subjected to only slight temperature fluctuations and, therefore, the mortalities observed at simulated condenser cooling temperatures are not surprising.

Once entrained in a condenser cooling system, the euphausiids would encounter an abrupt temperature increase of 12°-16°C (Coutant 1970), which could increase temperatures above the ambient temperature of Puget Sound to the critical range for survival. There are periods from July through September when surface temperatures may reach or exceed 15°C in portions of Puget Sound (Lincoln and Collias see footnote 2). Normally, surface temperatures do not exceed 14°C. Cooney (1971) noted high surface temperatures in June of 16.7°-19°C. These temperatures could result in condenser cooling temperatures of 27°C and above, which this study found to be 100% lethal in a very short time.

Data from this study indicate that even a short passage time through a condenser (15 min) at temperatures of 23°-24°C could kill from 11 to 53% of the euphausiids by thermal causes alone. The added loss due to abrasion, pressure, and toxic substances is unknown.

To minimize damage to the euphausiid populations, condenser cooling system intakes should be located deep enough to take advantage of the coldest cooling water available to minimize temperatures in the system. A very deep intake (just below 100 m) would probably minimize the entrainment of euphausiids. A surface intake would be especially harmful because of the higher surface temperatures and because of the swarming of euphausiids on the surface. Plant lights at night could cause the surface swarming.

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LUNAR SPAWNING OF THE THREADFIN, *POLYDACTYLUS SEXFILIS*, IN HAWAII[1]

Recent evidence indicates that lunar spawning rhythms are more common in fishes than was once thought. Johannes (1978) listed 50 species of teleost fishes with lunar spawning rhythms, most of them tropical and all of them marine or catadromous. In the course of developing methods for culturing the threadfin, *Polydactylus sexfilis* (Cuvier and Valenciennes), we found that this species displayed a lunar spawning rhythm (May 1976). The lunar pattern of spawning had been indicated by a previous field study (Lowell 1971) and is consistent with fishermen's lore (Hosaka 1944), but proof was lacking and details of the rhythm were unknown. In this paper we present detailed information on the lunar spawning of *P. sexfilis* along with observations of spawning behavior, using results from captive fish.

Polydactylus sexfilis is a much sought-after food fish in Hawaii and supports an important sport fishery as well as a small commercial fishery (Rao[2]). Information on the life history of this species (Lowell 1971; Morris and Kanayama[3]) indictates that spawning takes place close to shore. The larvae and juveniles lead a pelagic existence for about 3 mo, juveniles moving to shallow inshore areas at fork lengths (FL) between about 50 and 100 mm. The fish become sexually mature males at 20-25 cm FL and subsequently undergo a sex reversal, passing through a hermaphroditic stage and becoming functional females between 30 and 40 cm FL. Adults inhabit inshore rocky and sandy areas, frequently in zones of turbulence.

Methods

Juvenile *P. sexfilis* were captured by seine on reef flats along windward Oahu in September and October 1970 and reared to sexual maturity in tidal ponds at Coconut Island, in Kaneohe Bay, Oahu. The fish were daily fed chopped squid or smelt, commercial trout chow (40% protein), or trout chow supplemented with chopped squid. In May 1973, 30 mature fish (18 females and 12 males) were transferred to a 18-m^3 nylon net enclosure suspended from Styrofoam[4] floats and anchored off the leeward (southwest) side of Coconut Island. In June and July 1973, a small number of these fish were removed to laboratory tanks and used in experiments on hormone-induced spawning. During this work, ovarian biopsy samples were examined which contained residual eggs and indicated that the fish had been spawning spontaneously. In order to monitor any such spawning, an airlift egg collector was installed (May et al.[5]) in the center of the net in July 1973 and operated continuously (except for a few days when equipment malfunctioned) between 14 July 1973 and 31 December 1975. *Polydactylus sexfilis* produces pelagic eggs, so that the collector obtained a sample of eggs at each spawning. Every morning the entire contents of the collector were harvested and examined under a dissecting microscope, and the number of *P. sexfilis* eggs was estimated by sub-

[1]Contribution No. 552, Hawaii Institute of Marine Biology.

[2]Rao, T. R. 1977. Enhancement of natural populations of moi (*Polydactylus sexfilis*) in Hawaii through the release of hatchery-reared juveniles - a feasibility study of sea ranching. Univ. Hawaii, Hawaii Inst. Mar. Biol., Tech. Rep. 33, 46 p. Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, HI 96744.

[3]Morris, D. E., and R. Kanayama. 1964-69. Life history study of the moi, *Polydactylus sexfilis*. Job Completion Rep., Projects No. F-5-R-11 to F-5-R-17, Div. Fish Game, State of Hawaii. Division of Fish and Game, Honolulu, Hawaii.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5]May, R. C., G. S. Akiyama, and M. T. Santerre. 1976. A simple method for monitoring the spawning activity of fish in net enclosures. International Milkfish Workshop-Conference, May 19-22, 1976, Tigbauan, Iloilo, Philipp. Working Pap. 10, p. 133-138. Southeast Asian Fisheries Development Center, Kalayaan Building, Dela Rosa corner Salcedo Sts., Makati, Metro Manila, Philipp.

sampling. In 1976 and 1977, the collector was operated only during the spawning periods, which were predictable on the basis of data collected during the previous years. Eggs of *P. sexfilis* were distinguished from occasional eggs of other species by their diameter (800-825 μm) and by comparing hatched larvae with larvae obtained from hormone-induced spawnings; the identification was further corroborated by rearing larvae to the juvenile stage on several occasions. Since *P. sexfilis* undergoes a male-female sex reversal, additional males were added to the population each year to maintain a female to male sex ratio between 1:1 and 1.5:1 during the spawning season. In 1976, additional males were not added until the third spawning month, so data on spawning were not available for the first two spawning months of that year. At the end of this study in December 1977, the population of spawners numbered 57.

In order to determine the exact time of day when spawning occurred, water was sampled from the holding net continuously with a centrifugal pump at 10 l/min and passed through a small collecting basket (500-μm nylon mesh) on a barge anchored next to the net. The collecting basket was monitored visually, and the time when eggs first appeared was noted. The superstructure of the barge provided a barrier between the observer and the holding net, so that activities associated with monitoring the basket did not disturb the spawners in the net.

Results

Lunar Spawning Rhythm

Eggs of *P. sexfilis* were first observed in the collector from 23 to 25 July 1973. Subsequently the fish were found to spawn at night over a period of 3-7 (in one instance, 10) days once each month, always in proximity to the last quarter phase of the moon (Figure 1), and in a spawning season that extended from May or June to October (Table 1). Because the lunar month is 29.5 days long and does not coincide exactly with the calendar month, the calendar dates of spawning (Table 1) were generally 1-3 days earlier in each succeeding month. The first spawning of each monthly series was usually preceded by 1 or 2 days on which the fish fed less actively than normal. Counts of *P. sexfilis* eggs from the collector were made in August 1973, and thereafter. Judging from the samples obtained by the collector, relatively few eggs

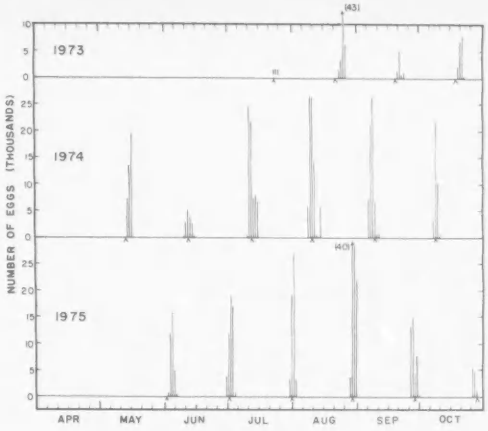

FIGURE 1.—Numbers of *Polydactylus sexfilis* eggs obtained by the airlift egg collector between August 1973 and October 1975. In July 1973, eggs were noted on 3 days but were not counted. Carets indicate the time of the last quarter phase of the moon.

TABLE 1.—Dates on which eggs were produced by captive *Polydactylus sexfilis* during study period. For each spawning month, the upper date is the first observed day of spawning, the lower date the last day.

Year	Spawning month					
	I	II	III	IV	V	VI
1973	(1)	(1)	(1)	22 Aug.	19 Sept.[2]	18 Oct.[2]
				25 Aug.	22 Sept.	21 Oct.
1974	13 May	9 June	9 July[2]	7 Aug.	5 Sept.	6 Oct.
	15 May	14 June	14 July	13 Aug.	10 Sept.	9 Oct.
1975	1 June[2]	29 June	29 July	27 Aug.	25 Sept.[2]	25 Oct.
	5 June	3 July	1 Aug.	30 Aug.	29 Sept.	27 Oct.
1976	(1)	(1)	17 July	15 Aug.	13 Sept.[2]	13 Oct.
			20 July	18 Aug.	16 Sept.	16 Oct.
1977	9 May	7 June[2]	6 July	4 Aug.	3 Sept.	1 Oct.
	14 May	11 June	11 July	13 Aug.	7 Sept.	5 Oct.

[1]Data not available.
[2]Collector malfunctioned on previous day; initial spawning day possibly earlier.

were produced on the first and last days of spawning, with a peak usually on the second or third day (Figure 1). However, because the eggs collected represented only a sample of the total number of eggs produced, it is possible that the peaks reflected some sampling variability.

The time of spawning relative to the lunar cycle appeared to change as the spawning season progressed. The first spawning series of the year always began (Figure 2) on the day of the last quarter (in one case the egg collector malfunctioned prior to the last quarter, and it is possible that the first day of spawning occurred earlier). In subsequent months the series began 1-4 days prior to

the last quarter (Figure 2). In April 1974 the collector obtained several thousand eggs over a 3-day period about 12 days before the last quarter; although the eggs were of the same diameter as *P. sexfilis* eggs, the larvae were not reared for positive identification. In view of the consistency of subsequent spawning data, and the low ovarian weights which two previous studies found in *P. sexfilis* in April (Lowell 1971; Morris[6]), we believe these were eggs of another species.

Some of the eggs found in the collector were transparent, buoyant, and developing normally, while others sank and were opaque and obviously not viable. Among the spawnings in which 1,000 or more eggs were collected, an average of 52% of the eggs were viable (range, 0-98%). The airlift collector apparently damaged the eggs to some extent. For example, on 13 June 1974, when 75% of the eggs from the collector were viable, eggs obtained by dip net at the time of spawning showed over 90% viability. It is not known how many of the fish in the net participated in each spawning or whether the same fish spawned each month, although Kanayama[7] believed that individual *P. sexfilis* spawned more than once in a season.

[6]Morris, D. E. 1964. Life history study of the moi, *Polydactylus sexfilis*. Job Completion Rep., Project No. F-5-R-11, Div. Fish Game, State of Hawaii, 15 p. Division of Fish and Game, Honolulu, Hawaii.

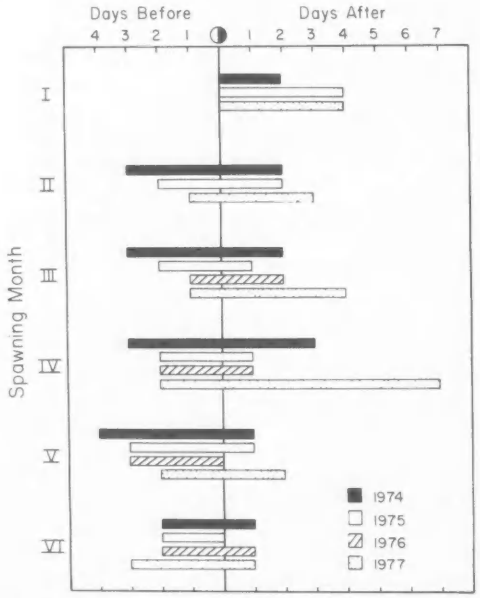

FIGURE 2.—Duration of spawning of *Polydactylus sexfilis* relative to the time of the last quarter (◑) for the six spawning months in 1974, 1975, and 1977. Data are given only for the last four spawning months of 1976.

Time of Spawning

The developmental stage of eggs found in the collector in the morning indicated that spawning had occurred shortly after sunset. Visual monitoring of water sampled continuously from the net on 34 spawning nights showed that with few exceptions the fish spawned between 2030 and 2130 h (Figure 3, Table 2). The times recorded were those when eggs were first observed in the collector; it is possible that additional spawnings took place slightly later on the same night, and behavioral observations (see below) indicated that this may have been true on at least some nights. The time of spawning did not vary with the time of sunset (Figure 3) and appeared unrelated to the time of moonrise (which occurred generally between 2300 and 0400 h during the spawning season).

[7]Kanayama, R. 1967. Life history study of the moi, *Polydactylus sexfilis*. Job Completion Rep., Project No. F-5-R-15, Div. Fish Game, State of Hawaii, 9 p. Division of Fish and Game, Honolulu, Hawaii.

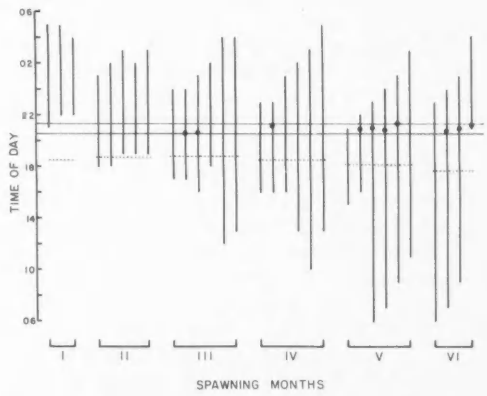

FIGURE 3.—Times of spawning of *Polydactylus sexfilis* during the six spawning months (roman numerals) of 1974 in relation to the tidal cycle. Dots indicate observed times of spawning in 1974, and the horizontal lines delineate the time of spawning as indicated by data from 1974, 1975, and 1977 (see Table 2). Dotted horizontal lines show the times of sunset in 1974. Vertical lines for each spawning night indicate time between the evening high and low tides, i.e., the duration of the outgoing tide, as measured by a tide gage at Coconut Island in 1974.

TABLE 2.—Times of first spawning in a captive population of *Polydactylus sexfilis* on nights in 1975 and 1977. Where a single time is given, the egg collector was examined continuously; in other cases, the collector was examined at intervals of 5-15 min. Numbers in parentheses indicate times of peak fish activity, presumed to be the exact time of spawning.

Date	Time of first spawning	Date	Time of first spawning
1975:		26 Sept.	2045-2100 (2052)
2 June	2115-2118	27 Sept.	2054-2100
3 June	2110-2115	28 Sept.	2050-2054 (2053)
4 June	2110-2115	29 Sept.	2135-2140 (2138)
5 June	2115-2120	26 Oct.	2050-2100 (2056)
30 June	2115-2120	27 Oct.	2105-2110 (2107)
2 July	2125-2130 (2127)	1977:	
3 July	2140-2145	7 June	2105
30 July	2045-2100 (2058)	9 July	2147
31 July	2120-2125	10 July	2140
28 Aug.	2115-2118 (2117)	6 Aug.	2050
29 Aug.	2129	4 Sept.	2103
30 Aug.	2115-2118 (2117)	3 Oct.	2038

Data from a tide gage located at Coconut Island were available for 1974 and showed that spawning nearly always took place on the outgoing tide (Figure 3). Although tide gage data were not available for subsequent years, tides predicted from tide tables showed patterns similar to the 1974 tide gage data. For 1975, 1976, and 1977, the time of spawning (i. e., 2030-2130 h) was compared with predicted tides and again found to occur mostly during the outgoing tide. Spawning occurred on the outgoing tide in 73% of the spawning nights during 1974-77.

Spawning Behavior

Observations of spawning behavior were made initially by watching bioluminescence caused by the fish's movement; later, direct observations were made by shining lights on the water at the time of spawning. The level of activity of the fish gradually increased beginning around 2015 h and culminated in the spawning act as determined by the appearance of eggs in the centrifugal pump samples. Occasionally the fish broke the surface of the water during the period of increased activity. During courtship the fish swam rapidly around the net in a circular manner in groups of two or three. They appeared to be chasing one another, and often one fish would contact another from behind, either dorsally or ventrally, with snout. Spawning appeared to take place between pairs rather than among larger groups of fish. Increased activity usually continued for 20 or 30 min after eggs were first noted.

Discussion

The captive population of *P. sexfilis* was clearly spawning with a well-defined lunar rhythm. Other evidence implies that this is a natural behavior for this species. Lowell (1971) set gill nets weekly in certain shoal areas of Oahu from April to August 1970 and reported that exceptionally large catches of *P. sexfilis* per effort occurred "after the full moon and continuing until the last quarter (1 week duration)," and because of the stage of gonadal development among fish in such catches, he termed them "spawning runs." In July 1970, female fish caught 3 days before the last quarter all had well-developed ovaries, but fish caught 4 days after the last quarter had spent ovaries. Fishermen seem to have been aware of the habits of *P. sexfilis* for a long time: Hosaka (1944:117) stated, "Moon light nights are best for moi (= *P. sexfilis*) fishing, and this is especially true when the moon is in the last quarter phase."

Spawning at the time of the last quarter phase of the moon appears to be rare among fishes. Of the 50 lunar spawners which Johannes (1978) listed, only two besides *P. sexfilis* spawned on the last quarter; both of these are species of *Amphiprion*, and one spawned on the first as well as the last quarter. Since the various species covered in Johannes' list occurred in different geographic locations, the variations in spawning days, taken together with variations in spawning times, could reflect local adaptations such as would occur if egg or larval survival were related to tides or currents.

The coincidence of spawning in *P. sexfilis* with the outgoing tide indicates that the remarkably precise timing of spawning may act as a mechanism for offshore dispersal of eggs and larvae. Lowell (1971) noted that there was a strong, oceanward current at his sampling site during falling tide, when he estimated spawning occurred, and results of ichthyoplankton surveys indicated that *P. sexfilis* eggs and larvae are not found in inshore waters in Hawaii (Leis and Miller 1976; Miller et al.[8]; Watson and Leis[9]). Johannes (1978)

[8]Miller, J. M., W. Watson, and J. M. Leis. 1973. Larval fishes. *In* S. V. Smith (editor), Atlas of Kaneohe Bay, a reef ecosystem under stress, p. 101-105. Univ. Hawaii Sea Grant Tech. Rep. 72-1. Sea Grant College Program, University of Hawaii, Honolulu, HI 96822.

[9]Watson, W., and J. M. Leis. 1974. Ichthyoplankton of Kaneohe Bay, Hawaii: a one-year study of the fish eggs and larvae. Univ. Hawaii Sea Grant Tech. Rep. 75-1, 178 p. Sea Grant College Program, University of Hawaii, Honolulu, HI 96822.

pointed out that spawning on outgoing tides is a common phenomenon among coastal marine fishes in the tropics, and he believed it evolved as a strategy for ensuring that eggs and larvae are transported away from the heavy concentration of predators in shallow water. Johannes noted that nocturnal spawning is also common in tropical reef fishes and serves to reduce predation both on the eggs and on the spawners.

The first *P. sexfilis* spawning of the year appears to be anomalous in that it occurs relatively late with respect to the last quarter. If offshore transport confers an important selective advantage on *P. sexfilis*, the lateness of the first spawning is maladaptive because it results in release of eggs early relative to the outgoing tide (see Figure 3). The initial phase of the spawning season may thus result in few viable offspring and could represent a gradual initiation of the main spawning season, delayed perhaps by the lower water temperatures which usually prevail during the first spawning month (Bathen[10]).

No observations on the spawning behavior of a polynemid fish have been published previously. In *P. sexfilis* the sexes apparently pair and spawn after a brief courtship involving rapid following and nosing of one fish by another. The spawning behavior of this species is similar in many respects to that of the Pacific bonito, *Sarda chiliensis*, including behaviors described by Magnuson and Prescott (1966) as "circle swimming," "tail nosing," and "following." The circling behavior noted among *P. sexfilis* may have been imposed by the confinement of the net enclosure, but *S. chiliensis* also showed tight circling behavior at the time of gamete release in a very large tank at Marineland of the Pacific, and circling prior to spawning occurs naturally in mullets (Helfrich and Allen 1975) and some (perhaps many) other tropical fishes (R. E. Johannes, Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, HI 96844. Pers. commun., December 1977). The circling behavior during spawning observed in captive *P. sexfilis* thus may not be abnormal for this species but may, as Magnuson and Prescott (1966) theorized for *S. chiliensis*, serve to enhance the probability of fertilization.

[10]Bathen, K. 1968. A descriptive study of the physical oceanography of Kaneohe Bay, Oahu, Hawaii. Univ. Hawaii, Hawaii Inst. Mar. Biol., Tech. Rep. 14, 353 p. Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, HI 96744.

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THE ROLES OF PRIOR RESIDENCE AND RELATIVE SIZE IN COMPETITION FOR SHELTER BY THE MALAYSIAN PRAWN, *MACROBRACHIUM ROSENBERGII*[1]

Behavorial dominance, territoriality, and their relationship to survival and population density have been the subject of extensive research (reviewed by Brown and Orians 1970; Itô 1970; Brown 1975). Generally dominance (behavioral) hierarchies imply some form of ranked order (reviewed by Marler and Hamilton 1966; Eibl-Eibesfeldt 1970; Itô 1970) whereby the alpha animal(s) has preferred access to food, shelter, or mates. Dominance may develop within a short time after an initial encounter (Dingle and Caldwell 1969), is partially controlled by differences in relative size (Marler and Hamilton 1966), and in some species is modified by relative location in space (Brown 1963). This latter modification is related to Noble's (1939) original concept of territory. Noble referred to territory as "any defended area." This area could serve as a "retreat" (in contrast to a sexual or nesting area) that "is occupied because it is familiar and defended because any newcomer is irritating to the resident."

Such space-related aggressive behavior has been reported in numerous animals (Brown and Orians 1970). Territorial behavior can be related to "defense" of 1) a breeding area (Buechner 1961; Watson 1964); 2) a renewable resource such as food (Stimson 1970); or 3) a physical shelter (Crane 1958; Reese 1964; Fielder 1965; Hughes 1966; Dingle and Caldwell 1969). Often the outcome of such a defensive action is exclusion of the intruder by the resident. Since this area is "familiar" to the resident and unfamiliar to the "newcomer," it follows that the resident has some type of advantage. This "prior resident effect" has been observed in a number of species (Braddock 1945, 1949; Miller 1958; Hughes 1966; Baird 1968; Dingle and Caldwell 1969; Selander 1970). Thus in many animals, spacing behavior is a powerful mechanism that can regulate resource utilization and influence distribution patterns.

Many of the above-mentioned studies and reviews dealt with animal populations in natural open systems subject to both immigration and emigration. In contrast, aquaculture systems are closed and deal with confined high-density populations. In the case of *Macrobrachium rosenbergii*, ponds are stocked with postlarvae, and harvesting of adults begins 9-12 mo later. The same space-related behavioral mechanisms observed in open systems may be operating in these high-density ponds. Circumstantial evidence indicates that this is occurring in ponds containing *M. rosenbergii*. Animals of the same age exhibit large variation in size at the end of several months of growth (Fujimura nad Okamoto 1970). Malecha (1977) reported that small *M. rosenbergii* can greatly increase their size when larger animals are absent. This has been called the "Bull Effect" by Fujimura and Okamoto (1970). Similar observations have been reported for carp (Nakamura and Kasahara 1955, 1961; Wohlfarth and Moav 1972), trout (Brown 1946), and salmon (Symons 1971). One hypothesis advanced by Nakamura and Kasahara (1961) is that the larger animals are outcompeting the smaller subordinates for food.

Macrobrachium rosenbergii is a large freshwater prawn. Its native distribution ranges from Pakistan to Papua, New Guinea, and Palau (Johnson 1960; McVey 1975). Usually it is found in fresh and brackish streams and pools. The eggs hatch near ocean waters, and the adults are found up to 200 km from the coast (Ling 1969). Generally males are thought to stay in upstream waters while the females undergo a seasonal migration, moving downstream and into brackish waters (Raman 1967). Relatively little is known of *M. rosenbergii's* behavioral ecology but Raman (1964) reported juveniles "hiding in crevices or among submerged plants along river banks." In order to understand how social behavior affects resource utilization by *M. rosenbergii*, three experiments were conducted in which shelter was the limiting resource, and relative size and prior residence were measured as variables.

Methods

The three experiments consisted of: a prior resident experiment, a simultaneous introduction experiment, and a control experiment. The prior resident experiment was used to test for the role of prior residence and relative size in competition for shelter. The simultaneous introduction experiment tested for the role of relative size on competition in the absence of a "prior resident effect." The control experiment tested for the effect of handling and capture.

[1]Contribution No. 544 from the Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, Hawaii.

Water conditions were maintained via an air lift filter. The animals were fed a dry pellet diet approximately every other day (see diet #5, Balazs et al. 1973). A 12-12 photoperiod with one-half hour twilight lighting at "sunrise" and "sunset" was employed.

Prior Resident Experiment

Earlier experiments revealed a form of shelter preference or selection operating in *M. rosenbergii* (Peebles 1977). The shelters used in this experiment were identical to those most frequently selected by animals in the earlier experiments. One shelter was placed in each experimental tank. A shelter consisted of six concrete bricks arranged into a double open ended square tunnel (19.3 × 19 × 11.4 cm tall).

Refuge other than the shelter was eliminated by the use of oblong experimental tanks (137 × 75 × 92 cm deep) and the suspension of the air lift filters just below the water surface (the usual position for these filters was on the bottom). Water depth was 34 cm.

Adults from commercial ponds were placed in two separate holding tanks, where they were kept for no longer that 1 wk. Two animals were removed, one each from the separate holding tanks. Three body characteristics were measured: standard length (tip of telson to orbit of eye), and lengths of left and right chelae. The animals were tagged by means of a small plastic "bread bag twist-tie" that was color coded and tied around the tail. It took about 15 s to attach. Following tagging the two animals were placed separately in experimental tanks. Three observations were made before the introduction of the "immigrant" and four observations were made after the introduction. The preintroduction observations were made on the second, third, and seventh days after the animals were placed in their separate experimental tanks. There were three observations per animal, each lasting 3 min. After the preintroduction week a coin was flipped to determine which animal would be the immigrant. The immigrant was designated as the introduced specimen and was moved via a dip net from its tank to the resident's tank. The resident was the animal that was not moved from one experimental tank to another. The postintroduction observations were made on the day of introduction, and the second, third, and seventh days after introduction. The observation performed on the day of introduction was 15 min and designed to monitor agonistic interactions associated with the initial encounters of the paired animals. The remaining three postintroduction observations were 3 min each and designed to record the animal's position within the tank. All observations were made between 1000 and 1530. Since these animals are nocturnal, movement and behavioral interactions were minimal during the daytime.

A total of 36 animals (18 immigrants, 18 residents) were used. Paired animals were of the same sex. This controlled for the possible confounding effect heterosexual courtship behavior might have on competition for shelter occupancy.

Simultaneous Introduction Experiment

The treatment of the simultaneous introduction experiment differed from the prior resident experiment in four ways: 1) only males were used; 2) the animals were simultaneously introduced into the oblong tanks; 3) two additional body characteristics were measured (body weight and carapace length); and 4) the animals were not separately observed prior to introduction.

Fifteen trials were run employing a total of 15 pairs or 30 animals. Observations were made on the day of simultaneous introduction, and the second, third, and seventh days after introduction. The observation performed on the day of simultaneous introduction was 15 min and designed to monitor agonistic interactions associated with initial encounters of the paired animals. The remaining three postintroduction observations were 3 min each and designed to record the animal's position within the tank.

Control Experiment

Eleven controls were run to test the effect of handling. Animals were selected, measured, tagged, and placed individually in experimental tanks. One week later the control was netted, held in the air, and reintroduced into the same experimental tank. Observations were made for the week before and the week after netting (mock immigration).

Operational Definitions

Successful: an animal that was in a shelter at the end of the 7-day period following immigration.

Unsuccessful: an animal that was not in a shel-

ter at the end of a 7-day period following immigration.

Push: an aggressive act where one animal pushes one of its chelae against the body of another animal.

Nip: an aggressive act where one animal closes down the tips of its chela on the body part of another animal.

Tête-a-tête: a type of aggressive act characterized by a head to head confrontation with at least one nip or one push. The tête-a-tête appeared to be difficult enough in orientation from the push and the nip to be placed in a separate category. Further observation and analysis might not support this separation.

Shove: an aggressive act where one animal holds both chela forward and parallel while charging into the flanks of another animal.

Bout: an agonistic exchange between two animals where at least one aggressive act occurred. A bout was considered terminated when aggressive acts stopped or one animal moved away and was not chased. Bouts were measured in units of aggressive acts.

Bout length: the number of aggressive acts that occurred during a bout.

Body characteristics: standard length (centimeters), right and left chelae length (centimeters), weight (grams), and carapace length (centimeters).

Body size index: the number of body characteristics in which an animal was larger. It was derived as follows: animal A larger than animal B in standard length and right chela length, then A's body size index is two. In the Prior Resident Experiment three body characteristics were measured, thus the maximum body size index in this experiment was three. In the Simultaneous Introduction Experiment five body characteristics were measured, thus in this experiment the maximum body damage index was five.

Results

Control Experiment

Ten out of 11 animals were in the shelter on every observation period before mock immigration. The remaining animal was in the shelter on one of the three observation periods. The same 10 were in the shelters on all observations following mock immigration, while the same remaining one was never observed in a shelter after immigration. It was concluded that the act of netting had no effect on shelter use.

Prior Resident Experiment

Shelters were occupied on every observation by every animal during the preimmigration week. Following immigration all shelters were occupied on every observation period. On several occasions more than one animal was in a shelter during the first two observation periods following immigration. However, by the end of the week, observation period 4, one animal was in a shelter while the other was usually at the opposite end of the tank. When the data were examined by immigrant versus resident for shelter use over the 7-day period, an interesting change became apparent (Figure 1). On the day of immigration, residents were occupying shelter significantly more often than immigrants (Binomial Test, $P = 0.044$, Siegel 1956). By the second observation period and for the remaining two observations there were no significant differences between residents and immigrants in frequency of shelter use (Binomial Test: day 2 after immigration, $P = 1.0$, day 3, $P = 0.814$; day 7, $P = 0.814$).

Examining the data for the effect of size (Figure 2) revealed that successful animals were significantly larger than their unsuccessful paired

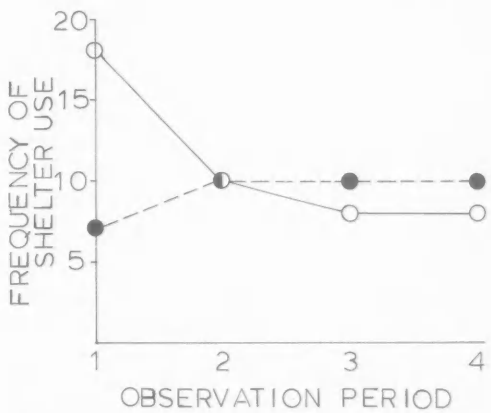

FIGURE 1.—Shelter usage by observation period for 18 pairs of *Macrobrachium rosenbergii*. The data from prior resident experiments are summed for the 18 pairs. During observation period 1, 18 residents (circles) and 7 immigrants (dots) were inside shelters. On observation period 1 there were seven cases of double occupancy; observation period 2, two cases; and observation period 3, none.

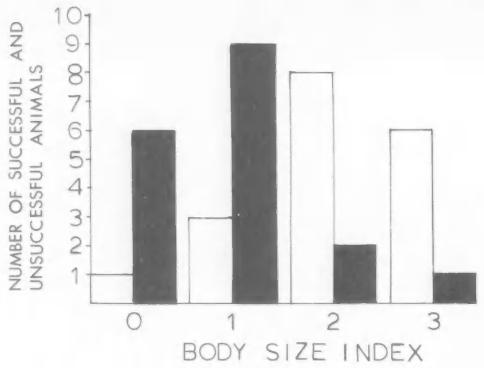

FIGURE 2.—Frequency of relative body size for successful (open bar) and unsuccessful (solid bar) prawns in the prior resident experiment. A body size index of one indicates one *Macrobrachium rosenbergii* was larger than the other in one body trait but smaller in the other two body traits.

partners (Kolmogorov-Smirnov Two Sample Test: D max $= 11, n = 18, P = 0.01$).

Simultaneous Introduction Experiment

A similar effect of size on shelter use was observed in the simultaneous introduction experiment (Figure 3; $r_s = 0.579, P<0.001$). Once again larger animals used the shelters more often than their smaller partners.

Aggressive behavior was observed only on the day of introduction. The nip and push occurred more often than the shove or tête-a-tête (Figure 4). Generally aggressive interactions were limited to a few (one to three) bouts per 15 min (Figure 5), and these bouts were usually one or two aggressive acts long (Figure 6).

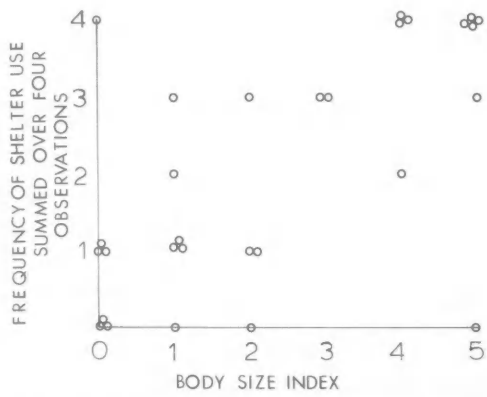

FIGURE 3.—Correlation between frequency of shelter use and body size index for *Macrobrachium rosenbergii*, from the simultaneous introduction experiment. A body size index of one indicates one animal was larger than the other in one body trait but smaller in the other four body traits.

Prior Resident Experiment by Simultaneous Introduction Experiment

A Kolmogorov-Smirnov chi-square approximation (Goodman 1954; Siegel 1956) revealed that animals of the simultaneous introduction experiment were more aggressive on the day of introduction than were animals in the prior resident experiment on the day of immigration ($\chi^2 = 15.54$, $P<0.002$ for number of bouts/animal per 15-min period; $\chi^2 = 13.877$, $P<0.002$ for number of ag-

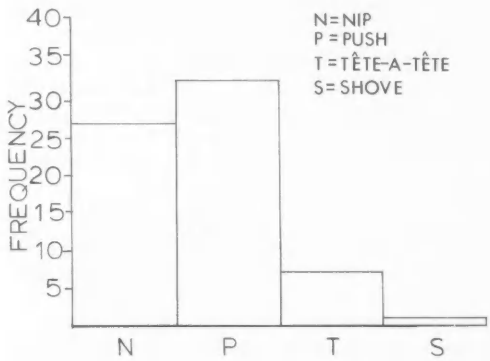

FIGURE 4.—Frequency by type of aggressive acts observed on the first day after introduction for the experiment on simultaneous *Macrobrachium rosenbergii* introduction. Frequency equals the number of aggressive acts by 17 animals.

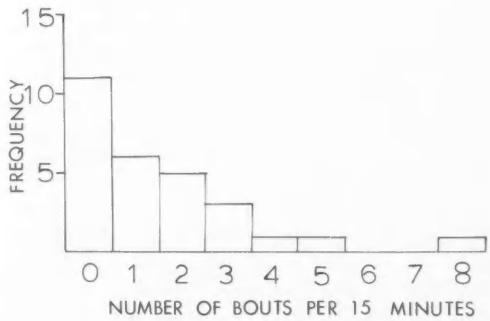

FIGURE 5.—Frequency of number of aggressive bouts per animal during the 15-min period of observation after simultaneous introduction of male *Macrobrachium rosenbergii* (14 pairs).

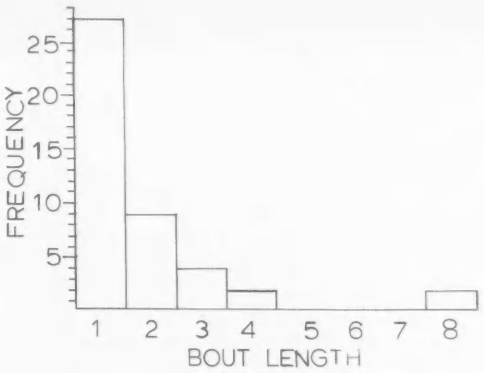

FIGURE 6.—Frequency of bout length (number of aggressive acts per bout per animal) for the simultaneous introduction of 14 pairs of male *Macrobrachium rosenbergii*.

gressive acts/animal per 15-min period). Simultaneous introduction animals exhibited a total of 68 aggressive acts occurring in 43 bouts (n = 28 animals), while the prawns from the prior resident experiment exhibited only five aggressive acts in five bouts (n = 32 animals).

Discussion

The results indicate that when *M. rosenbergii* compete for shelter at least three factors, relative size, prior residence, and length of time contestants are paired, play important roles in determining who occupies a shelter. It has long been recognized that in crustaceans relative size plays a large role in determining dominance (Allee and Douglas 1945; Bovbjerg 1953, 1956, 1960; Lowe 1956). More recent observations have confirmed the size/dominance relationship (Hughes 1966; Crane 1967; Griffin 1968; Hazlett 1968; Dingle and Caldwell 1969; Warner 1970; Rubenstein and Hazlett 1974; Jachowski 1974; Molenock 1976; Sinclair 1977). However, relative size does not appear equally important in all species (Hazlett and Estabrook 1974).

In prawns, relative size strongly influences the outcome of competition. When two prawns encounter one another in an area new to both, the larger animal usually has the advantage. Often these encounters are characterized by a limited series of pushes with one or the other chela. The function of the pushing might be threefold: 1) to test their opponent's weight (rest inertia), 2) to determine the opponent's molt state, and 3) to see if the opponent is capable of pushing back (has chelae). Other crustaceans appear to measure their opponent's physical strength by means of physical interactions involving the chelae (Griffin 1968; Schöne 1968). In *Cambarellus shufeldtii*, claw removal causes dominant animals to drop in rank (Lowe 1956). In *M. rosenbergii* deaths related to agonistic behavior usually occurred near ecdysis and often the first appendages lost during an agonistic encounter were the chelae (Peebles 1977).

Smaller animals have been observed successfully defending shelters from attempted occupation by larger congeners (Bovbjerg 1953; Griffin 1968; Sinclair 1977). This is related to the prior resident phenomenon and it is central to Nobel's (1939) definition of territory. Resident *M. rosenbergii*, regardless of their relative size, successfully retained their shelters. The mechanism the residents employed apparently was not limited to direct physical interaction. Immigrants and residents seldom fought. Generally immigrants were inactive upon placement into a tank housing a resident. The immigrant's aggressive behavior was well below its counterpart in the simultaneous introduction group. Only occasionally (Figure 1) did the immigrant seek out the shelter. This latter behavior is in direct contrast to the control group. A control group animal was usually back in its shelter within 1 min after reintroduction. Possibly an exocrine was an agent of communication between resident and immigrant prawns, since a novel environment did not inhibit exploration in animals of the simultaneous introduction experiment; and animals from the control experiment reintroduced into tanks contaminated with their own exocrines, rapidly entered their shelter.

The advantage conferred upon resident *M. rosenbergii* appears to disappear within a short period of time. The smaller resident can defend its shelter against intrusion for no longer than a few days (Figure 1). Apparently relative size can overcome the prior resident effect if resident and immigrant continue to encounter one another. Similar observations were reported by Lowe (1956). In the case of the *C. shufeldtii*, a dominance hierarchy was established before shelters were introduced. Dominant *C. shufeldtii* displaced subordinates from occupied shelters. In my experiments, *M. rosenbergii* first exhibited territoriality as determined by the presence of the prior resident effect. Territoriality then broke down, due to continued encounters, into simple dominance.

The important point addressed in this paper is not who wins or loses the encounter but which animal gains access to the resource. Investigators whose observations were limited to the first encounter might suggest that residents almost always outcompete intruders for shelter. However, I have shown that in a closed system the prior resident effect breaks down into simple size-related dominance. These results offer a behavioral explanation for the known and recognized bull effect in prawn aquaculture ponds. Larger animals have preferential access to food and shelter, two important resources which are often dispersed in a clumped or patchy fashion.

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PRINCIPAL SPAWNING AREAS AND TIMES OF MARINE FISHES, CAPE SABLE TO CAPE HATTERAS

The purpose of this compendium is to summarize spawning areas and seasons of the more abundant marine fishes of the continental shelf between Cape Sable, N.S., and Cape Hatteras, N.C., as an aid to the identification of fish eggs and larvae and planning and scheduling ichthyoplankton surveys. We have used the term "marine" to encompass fishes which spawn at sea (in contrast to estuarine spawners), although some of the species included spawn in both environments contingent on geographic location (e.g., winter flounder which spawn exclusively in estuaries in the Middle Atlantic Bight and offshore in the Gulf of Maine and Atlantic menhaden which spawn in estuaries along southern New England and in the New York Bight and offshore in the lower Middle Atlantic Bight and in the South Atlantic Bight).

The Gulf of Maine is defined as the oceanic bight bounded by Nantucket Shoals and Cape Cod on the west (long. 70°W) and Cape Sable on the east (long. 65°W) including Georges and Browns Banks and waters out to the 200-m contour (Colton 1964). The Middle Atlantic Bight is the area

inshore of the continental slope bounded by Cape Cod and Nantucket Shoals to the east (long. 70°W) and Cape Hatteras to the south (lat. 35°N). The New York Bight, as defined in the MESA New York Bight Atlas Monograph Series (Bowman and Wunderlich 1977), is the offshore water area in the bend of the Atlantic coastline from Long Island (long. 71°30′W) to New Jersey (lat. 38°30′N). A chart of the Gulf of Maine and Middle Atlantic Bight and the names of places and areas referred to in the spawning summary are given in Figure 1.

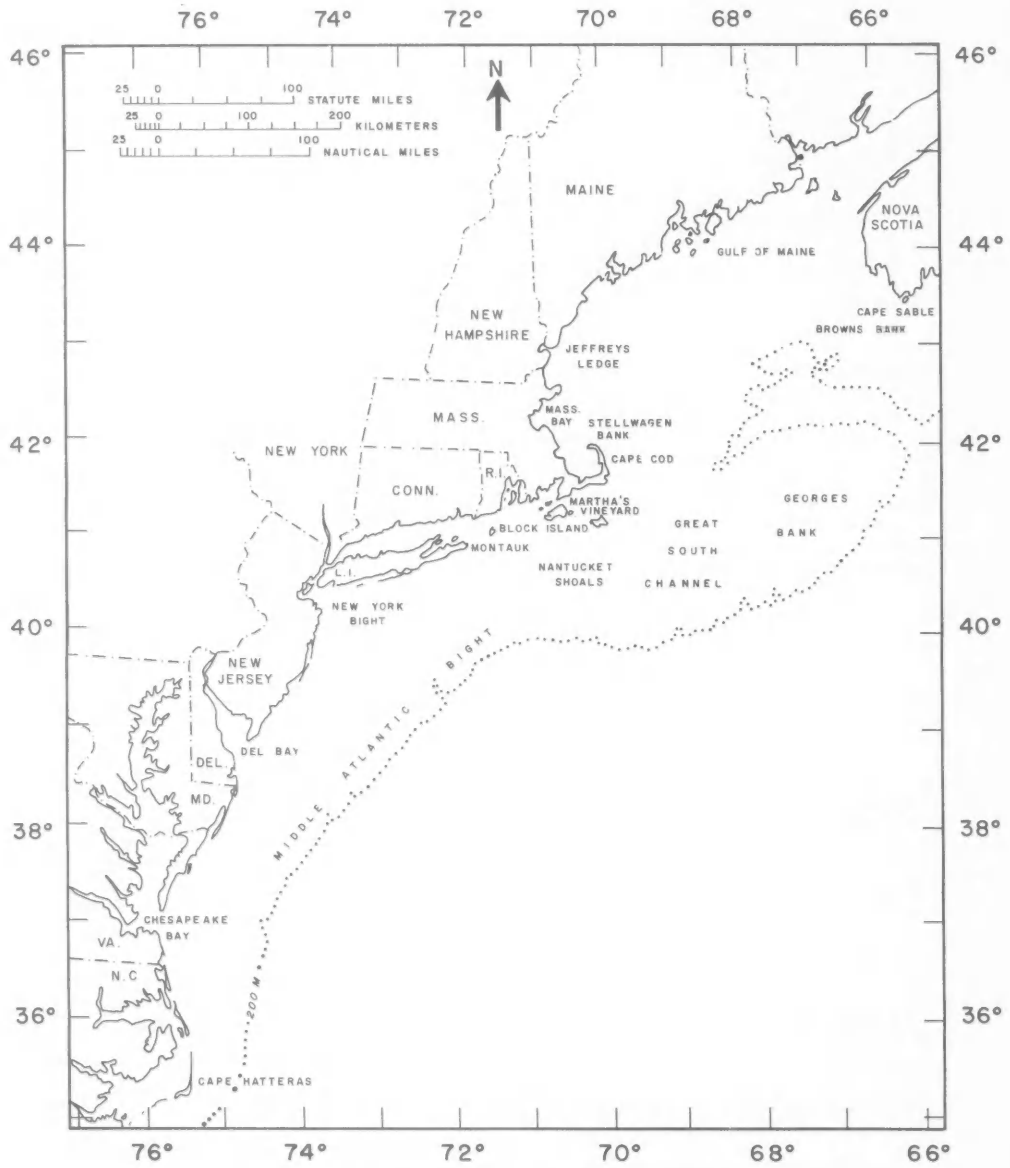


FIGURE 1.—Orientation chart of the Gulf of Maine and Middle Atlantic Bight.

In this summary (Table 1) we have treated the Gulf of Maine and the Middle Atlantic Bight separately for there is an abrupt general division between the biological and physical properties of water east and west of Cape Cod. The boreal waters over most of the Gulf of Maine are well mixed by strong tidal currents, while the circulation of the warmer shelf waters west of Cape Cod is more sluggish, and its chemical and physical properties are less complex (Colton 1964). The offing of Cape Cod also appears to be a definite transition zone (probably thermal) for some northern and southern species of fishes and invertebrates, both pelagic and benthic (Colton 1964). The species composition and abundance of fishes vary markedly between the two regions, with boreal, nonmigratory species dominating the Gulf of Maine and warmwater, migratory species prevailing in the Middle Atlantic Bight. The bulk or total spawning of many species of fishes is restricted to areas east (e.g., haddock, pollock, redfish) or west (e.g., bluefish, menhaden, anchovies) of Nantuck-

TABLE 1.—Principal spawning areas and times of marine fishes, Cape Sable to Cape Hatteras.

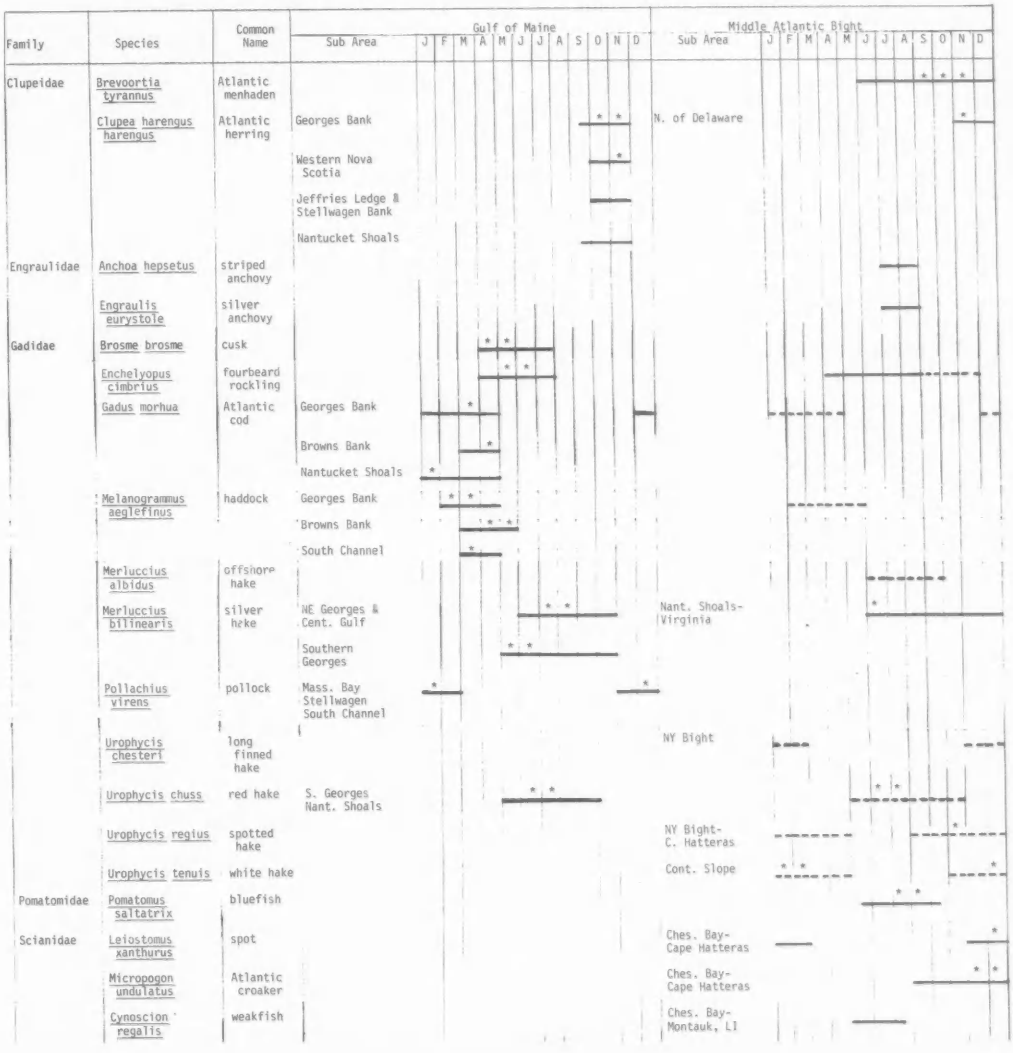
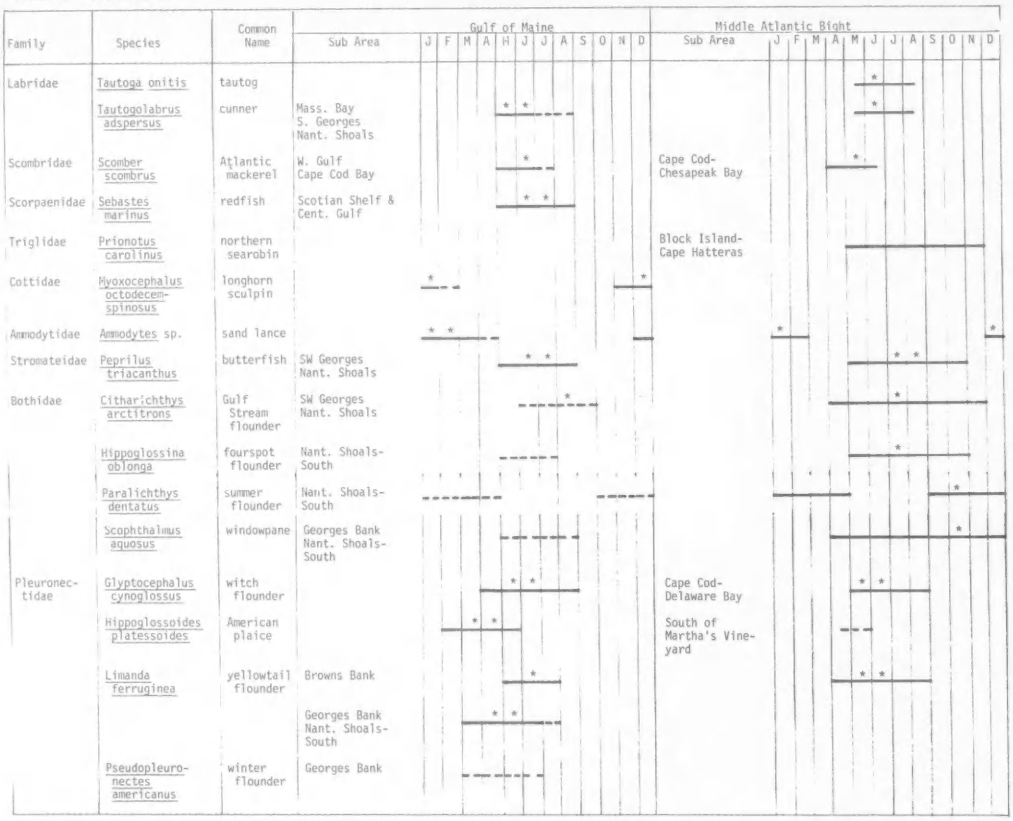


TABLE 1.—Continued.



——— Known spawning season.

- - - - - - - Uncertain spawning season.

*Peak spawning.

et Shoals, although there are exceptions to this general rule (notably, yellowtail flounder and silver hake).

The spawning summaries are based primarily on published data collected on Bureau of Commercial Fisheries (now National Marine Fisheries Service) ichthyoplankton surveys of the Gulf of Maine and Middle Atlantic Bight made in the 1950's and 1960's and listed in the References. Published data from earlier studies (e.g., Fish 1929; Walford 1938; Pearson 1941; Sette 1943; Bigelow and Schroeder 1953) and some unpublished information from more recent National Marine Fisheries Service ichthyoplankton surveys have also been utilized. We have not attempted to make the bibliography encyclopedic. However, the papers cited include references to all pertinent spawning summaries. Spawning areas and seasons were determined on a basis of the occurrence of eggs and/or early stage (yolk-sac) larvae. The families are arranged in phyletic sequence (Greenwood et al. 1966) and the species are listed in alphabetical order. Common names follows those recommended by Bailey et al. (1970).

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RECENT SIGHTINGS OF THE BLUE WHALE, *BALENOPTERA MUSCULUS*, IN THE NORTHEASTERN TROPICAL PACIFIC

The blue whale, *Balenoptera musculus*, in the North Pacific, migrates to the Gulf of Alaska and Aleutians in the summer for feeding (Nishiwaki 1966). It is believed to migrate to tropical waters in winter for calving, but sightings of blue whales in lower latitudes are rare (Tomilin 1957). In mid-July 1928, Cruikshank reported seeing ". . . several blue whales . . ." at lat. 11°32′N and long. 91°58′W (Kellogg 1929). A Peruvian fishery reported taking 247 blue whales between December 1925 and March 1926 (Ingebrigtsen 1929). Potentially these were from a North Pacific stock, since the Southern Hemisphere blue whale is most numerous in the Antarctic at this time. Volkov and Moroz (1977) noted an abundance of baleen

whales between lat. 7° and 10°N. Although individual species of baleen whales were not enumerated by Volkov and Moroz, two sightings of blue whales were made on 29 March 1975 and are presented here (Table 1, *Vnushitelnyi* cruise).

Typically blue whales are seen along the Baja California coast in October while migrating southward, and subsequently reappear off Baja California in large numbers in March-June on their northward migration (Rice 1974). The whereabouts of the North Pacific blue whales during the winter months is completely unknown, but this is probably due to the lack of sighting effort. For instance, Japanese whale scouting has been carried out systematically since 1965, but their effort has been restricted to the Pacific waters north of lat. 20°N (Wada 1977).

Two theories have evolved regarding the wintering grounds of the blue whale. Wheeler (1946), suggested that blue whales winter within a limited area of the subtropics. He maintained that whales congregate in large groups in areas not frequented by vessels. A second theory maintains that wintering blue whales disperse between the feeding grounds and the tropics (Harmer 1931; Mackintosh 1942). Presented in this note is a 3-yr record of blue whales sighted in the northeastern tropical Pacific. Reference is made to migration, whale groupings, behavior, and to the oceanographic features of the sighting area. These recent sightings were made by trained observers aboard vessels involved with the National Marine Fisheries Service Tuna/Porpoise Research Program. Sighting information from other experienced observers has also been contributed.

Shipboard identification of rorquals is difficult and this problem was compounded by the fact that most of the sightings mentioned in this paper were incidental to ship's activities. However, the blue whale is easily discerned from other rorquals by the recognition of the following combination of characteristics:

1. Mottled blue-grey coloration. All other rorquals are uniformly steel grey on the dorsal surface.
2. A small dorsal fin of varying shapes located in the posterior third of the body. The dorsal fin of the sei, fin, and brydes whales is larger, falcate shape, and placed farther anterior than the blue whale dorsal fin.
3. A U-shaped rostrum. The rostrum shape of other balenopterids is more pointed.
4. Tall, dense, disperse blows. Generally, the blow of the sei and brydes whales is low and dissipated, while the fin whale has a tall conical-shaped blow.

A total of 11 cruises are discussed in this report, covering the period from January to May for 1971, 1975, 1976, and 1977.[1] The area of effort and sightings of blue whales are reported in Figure 1. The

[1]No blue whale sightings were made in 1977, although two cruises have been included in Figure 1 to complement survey effort.

TABLE 1.—Annotated list of blue whale sightings by National Marine Fisheries Service observers in the northeastern tropical Pacific, January-May 1971-76.

Date	Lat., Long.	No. of whales	Observations	Cruise/Observer
8 Jan. 1971	07°54'N, 095°52'W	1		*Nautilus*/Leatherwood
23 Jan. 1975	01°30'N, 083°04'W	1	Dove for 7 min	*Pan Pacific*/Friedrichsen
3 Feb. 1975	07°29'N, 093°48'W	cow and calf	3 dives, 5.57 min/dive; length: cow 27 m, calf 8-10 m	*Aquarius*/Wade
4 Feb. 1975	07°48'N, 097°40'W	1	Surfaced in middle of tuna school	*Finesterre*/Walker
7 Feb. 1975	07°45'N, 098°21'W	1	5 dives, 10.11 min/dive	*Aquarius*/Wade
7 Feb. 1975	07°47'N, 098°24'W	1	2 dives, 8.19 min/dive	*Aquarius*/Wade
7 Feb. 1975	07°52'N, 098°47'W	2	Small unidentified whale, 10 m, with visible blow, swimming with a large blue whale	*Aquarius*/Wade
7 Feb. 1975	07°47'N, 099°00'W	1	3 dives, 11.39 min/dive; exposed tail fluke on all dives	*Aquarius*/Wade
9 Feb. 1975	08°50'N, 096°04'W	4-6	Paired groups, length estimate: 27 m	*Pan Pacific*/Friedrichsen
10 Feb. 1975	08°33'N, 096°47'W	1		*Pan Pacific*/Friedrichsen
15 Feb. 1975	08°36'N, 096°29'W	1		*Pan Pacific*/Friedrichsen
17 Feb. 1975	08°58'N, 096°54'W	8-10	Mostly pairs dispersed over several square miles; all headed northeast	*Pan Pacific*/Friedrichsen
17 Feb. 1975	08°53'N, 096°36'W	1		*Pan Pacific*/Friedrichsen
29 Mar. 1975	08°55'N, 093°34'W	10-13		*Vnushitelnyi*/Rice
29 Mar. 1975	09°07'N, 093°55'W	6-7		*Vnushitelnyi*/Rice
13 Feb. 1976	09°44'N, 092°25'W	2		*Cromwell*/Friedrichsen et al.
13 Feb. 1976	09°44'N, 092°31'W	1	Length estimate: 23 m	*Cromwell*/Friedrichsen et al.
13 Feb. 1976	09°44'N, 092°35'W	4-5	Whales dispersed over 4-5 mi^2	*Cromwell*/Friedrichsen et al.
13 Feb. 1976	09°44'N, 092°52'W	1	Exposed tail flukes prior to sounding	*Cromwell*/Friedrichsen et al.
28 May 1976	10°31'N, 092°45'W	1	Length estimate: 20 m	*Martinac*/Friedrichsen

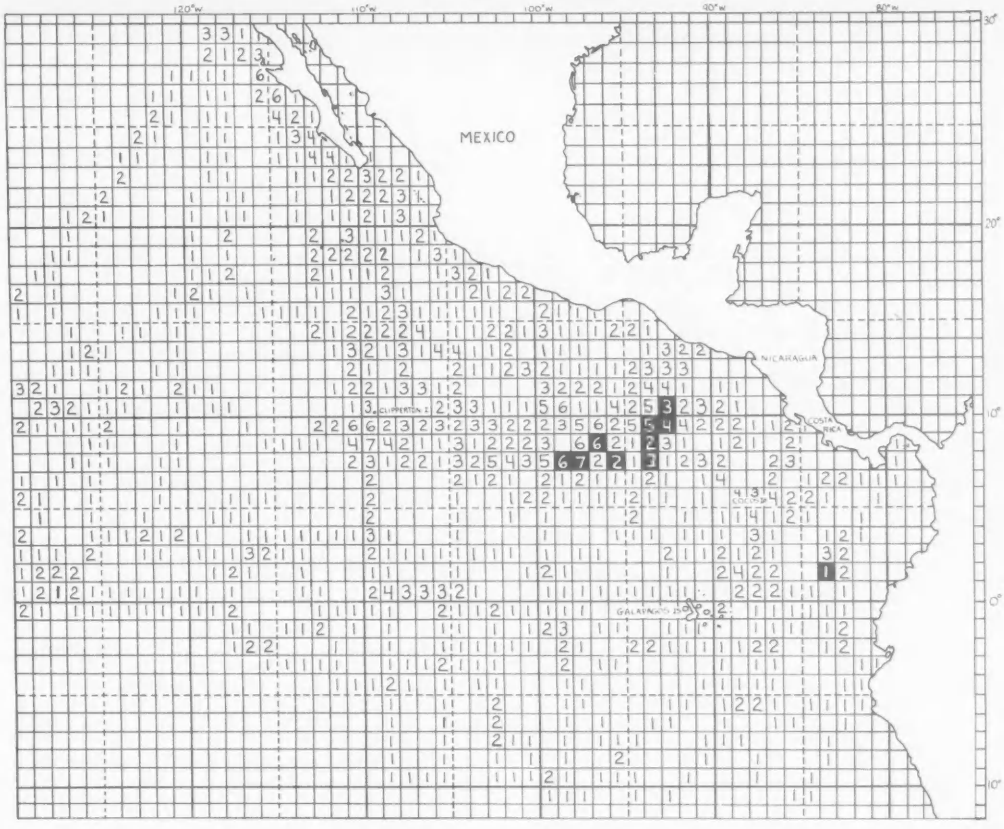

FIGURE 1.—Survey effort for blue whales in the northeastern tropical Pacific over 11 cruises from January to June in 1971, 1975, 1976, and 1977. Each numeral represents the total number of times that vessels entered a 1° block. Darkened blocks indicate blue whale sightings.

fact that blue whales have been sighted in the same general area for three winters indicates that North Pacific blue whales may have a distinct wintering ground to which they migrate each year.

The location of the suggested wintering grounds indicated by the sighting data are lat. 7°29′-10°31′N and long. 95°25′-99°00′W.[2] Only 1 of the 20 blue whale sightings (lat 1°30′N and long. 83°04′W, 23 January 1975, a solitary individual) was outside of these bounds. The equatorial sighting location of this whale may indicate that either it was not from the North Pacific population, or that North Pacific blue whales do not restrict migration to the hypothetical wintering grounds.

[2]Cruikshank's observations, in 1928, were also in this area.

Whale Groupings and Behavior

Blue whales are believed to be found singly or in pairs (Leatherwood et al. 1976). In fact, Nemoto (1964) reported that blue whales observed on the summer feeding grounds were solitary. However, five of the sightings reported here were aggregations of whales dispersed over several square miles. Many of the whales were paired. The multiple sightings on 7 February 1975 and 13 February 1976 appear to be mostly of solitary animals (Table 1). However, on both days, no less than 40 n.mi. separated the first and last whales sighted. Also, four out of the five whales observed on 7 February 1975 were headed in a northeasterly direction. This information may indicate that these apparently solitary whales were part of a large dispersed group.

At least one cow and calf were observed and possibly a second pair (Table 1). This is the first actual record of a blue whale calf in the tropics, although historically it has been believed that blue whales have their calves in the warm tropical waters (Mackintosh 1966:126).[3]

Oceanographic Features

There are several unique oceanographic features which relate to the sighting location of the blue whales. Cromwell (1958) and Wyrtki (1964) discussed the Costa Rican Dome which is located at approximately lat. 9°N, long. 89°W. The dome is apparently a permanent topographic feature (150 km × 300 km) and is formed by the convergence of several major current systems. These currents typically create an area of nutrient transport or upwelling. High standing stocks of zooplankton in the area near the Costa Rican Dome (lat. 7°25′N-10°N) has been reported by several authors (Reid 1962; Blackburn et al. 1970; Holmes[4]). Volkov and Moroz (1977) suggested that the high stable food base of the area creates a habitat suitable for nonmigratory populations of baleen whales. North Pacific blue whales may also use this area for their winter feeding grounds.

In conclusion, the recent sightings of blue whales in the tropics indicates that North Pacific blue whales have a wintering area to which they return each year. Since most of the cruises have occurred largely during the winter months, more information must be collected to determine if whales are found in this area the year round. The high standing stock of zooplankton in this area may indicate that this is a winter feeding area, as well as a calving ground.

Acknowledgments

We are particularly indebted to E. D. Mitchell, Fisheries Research Board of Canada, for his critical evaluation of the manuscript. D. W. Rice, National Marine Fisheries Service; K. S. Norris, University of California at Santa Cruz, and Ron Garrett, Wilderness Research Institute, also made helpful suggestions on the draft. We also thank Steve Leatherwood, W. A. Walker, and D. W. Rice, who contributed blue whale sighting data and Karen J. Rice for technical assistance. Last, we thank Robert Schoning of the National Marine Fisheries Service for releasing this data for publication.

[3]The average water temperature for 11 sightings was 26.5°C.

[4]Holmes, R. W. 1970. A contribution to the physical, chemical, and biological oceanography of the northeastern tropical Pacific. (Unpubl. manuscr.) Institute of Marine Resources. Scripps Institute of Oceanography, Univ. Calif. La Jolla, Calif. AEC-UCSD-34P99-4.

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SEX COMPOSITION, LENGTH-WEIGHT RELATIONSHIP, AND REPRODUCTION OF THE WHITE MARLIN, *TETRAPTURUS ALBIDUS*, IN THE WESTERN NORTH ATLANTIC OCEAN[1]

In the Atlantic, white marlin, *Tetrapturus albidus*, range from lat. 35°S to 45°N with concentrations in the western Atlantic, including the Gulf of Mexico, and the Caribbean Sea (Mather et al. 1975). Tag returns show that some white marlin migrate seasonally from the U.S. Middle Atlantic Bight (the coastal area between Cape Cod and Cape Hatteras) in the summer to the southeastern Caribbean Sea in the winter (Mather et al. 1972). Commercial catches by Japanese longline vessels support the tagging results, but the catches also indicate that a second group of white marlin moves from a wintering area in the southeastern Caribbean to summer grounds in the Gulf of Mexico (Ueyanagi et al. 1970; Mather et al. 1972; Wise and Davis 1973).

A substantial sport fishery exists for white marlin in the Atlantic off North and South America. In the United States, the major sport fisheries occur along the Middle Atlantic States, from New Jersey to North Carolina, off southeast Florida, and along the Gulf Coast States. Important sport fisheries also occur in the Bahamas, off Havana, Cuba, and along the coast of Venezuela (Mather et al. 1972). Another important sport fishery recently developed off eastern Brazil (Anonymous 1976).

The white marlin is also an incidental catch of commercial longline vessels fishing for tuna in the Atlantic and Gulf of Mexico (Mather et al. 1975). The marlin is highly prized as a food item in some countries (Kume and Joseph 1969).

My review of the literature on white marlin shows that there is a need for additional information on sex composition and length-weight relationships. Until recently, no information was available regarding its reproductive potential (Baglin[2]). In this paper I update reproductive and sex ratio data presented by Baglin (see footnote 2) and include length-weight relationships.

Materials and Methods

White marlin from the northern Gulf of Mexico (hereafter referred to as the gulf), the Florida Straits, the western Bahamas, and the Middle Atlantic Bight of the western North Atlantic (hereafter referred to as the Atlantic) were sampled from anglers' catches at sport fishing tournaments and at Pflueger Marine Taxidermy, Inc., Hallandale, Fla. One marlin was collected by longline in the Windward Passage between Cuba and Hispaniola during RV *Oregon* Cruise 66.

Sex data were obtained from 1,128 white marlin captured by anglers in the gulf (1971-77) and from 720 white marlin caught by anglers from the Atlantic (1972-77).

Lengths and weights were obtained from 904 white marlin captured in the gulf (1971-76) and from 489 white marlin captured in the Atlantic (1972-76). Body lengths (straight distance from tip of lower jaw to tips of midcaudal rays) were measured in centimeters (Rivas 1956); weights were recorded to the nearest pound and converted to kilograms.

[1]Contribution No. 78-44M, Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, Miami, Fla.

[2]Baglin, R. E., Jr. 1977. Maturity, fecundity and sex composition of white marlin (*Tetrapturus albidus*). Collective Volume of Scientific Papers 6(79):408-416. International Commission for the Conservation of Atlantic Tunas, Madrid, Spain.

Ovaries from 186 females caught from 1972 through 1976 were examined. Fresh ovaries were either blotted dry and weighed in grams or stored in 10% Formalin[3] and weighed later. No significant difference was found between the mean weight of fresh and preserved ovaries ($F = 0.0001$; df = 1, 16; $P > 0.75$). The gonosomatic index (GSI), ovary weight as a percentage of total body weight, was used as an indicator of maturity.

Preserved eggs 0.56 mm in diameter and larger were counted when estimating fecundity. Eggs <0.56 mm were less spherical in shape and in an earlier stage of development. The 0.56-mm size was determined by measuring the diameters of 3,912 eggs from mature, partly spent, and spent fish. Small transparent ova were stained with aceto-carmine to facilitate measuring. Egg diameters were measured with an ocular micrometer at 30× magnification and the orientation of egg diameters was assumed to be random. Thin cross sections were taken from the anterior, middle, and posterior parts of one ovary of a mature fish and subdivided into three subsamples, representing the center, midregion, and periphery of the ovary (Otsu and Uchida 1959).

Fecundity was defined as the potential number of mature eggs (yolked ova in the most advanced size mode) that could be spawned during one reproductive season and was estimated using a dry weight method. For six fish in which entire ovaries were saved for fecundity analysis, subsamples consisted of a thin cross section taken from the anterior, middle, and posterior parts of each ovary. The eggs in these subsamples were separated from the ovarian tissue, enumerated, dried, and weighed according to the procedure described by Baglin (see footnote 2). For six other fish, only the ovary weight and a single cross section from the middle of the ovary were taken; these cross sections comprised the subsamples. The eggs were separated, counted, dried, and weighed. A dry/wet weight regression was used to estimate the total dry weight of the eggs in these ovaries, which were not saved. Before the eggs in the subsample were counted, 25 eggs 0.30 mm and larger from the two most advanced modes were randomly selected and measured. Eggs in this second most advanced mode were included to give an indication of the percentage of eggs in both modes because future histological studies may indicate that these smaller eggs undergo further development and are also spawned. Fecundity estimates, rounded to the nearest 0.1 million eggs, were calculated from the relationship: $C = (AD/B) + A$, where A is the number of mature ova in the subsample, B is the weight of the ova in the subsample, C is the number of mature ova, and D is the weight of ova from both ovaries.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results and Discussion

Sex Composition

From 1971 through 1977, sex was determined from 1,128 white marlin from the gulf (Table 1). The deviation from an expected 1:1 sex ratio was significant from May through October. Sampling was inadequate for the remaining months. Females were more prevalent than males for each month studied.

From 1972 through 1977, sex was determined for 720 white marlin from the Atlantic (Table 1). There were 323 sex determinations from the Florida Straits (March through May) and 397 from the Middle Atlantic Bight (June through September). Sampling was inadequate from October through February. No significant difference from an expected 1:1 sex ratio was found for March, May, July, August, and September, but a significant difference was found for April and June. For the months in which the sex ratio was significantly different from the expected 1:1 ratio, females were more prevalent.

deSylva and Davis (1963) found a significant difference from an expected 1:1 sex ratio (60% females) when they combined their data from the Middle Atlantic Bight for the summers of 1959 and 1960. They presented monthly sex composi-

TABLE 1.—Monthly sex ratios for white marlin from the northern Gulf of Mexico (1971-77), Florida Straits and Middle Atlantic Bight (1972-77).

Location	Month	Number of white marlin	Sex ratio (females/males)
Gulf of Mexico	May	21	4.25*
	June	85	4.00*
	July	374	3.16*
	August	444	1.63*
	September	150	1.50*
	October	54	1.84*
Florida Straits	March	103	0.87
	April	172	1.96*
	May	48	1.40
Middle Atlantic Bight	June	55	3.23*
	July	56	1.67
	August	219	0.80
	September	67	0.97

*Significant departure from null hypothesis at 0.05 level (chi-square).

tion data for 1960 only. My analysis of their data shows a significant difference for June and July but no significant difference for August and September. Their findings for June, August, and September agree with those in this study. The extreme difference in sex ratios found in the present study for the gulf (May through October) and for the Florida Straits in April has not been reported previously. The above findings suggest that some white marlin segregate into distinct areal groups according to the predominating sex and that sex ratios may change with season. A similar occurrence has been noted for the blue marlin, *Makaira nigricans* (Kume and Joseph 1969).

Length-Weight Relationship

The average length of females is greater than that of males from both the gulf and the Atlantic (Figure 1). It is also apparent (Figures 2, 3) that the average length of females is greater than that of males from each area for each month studied. This difference may be due to faster growth of females or higher mortality of males and should be considered in future growth studies of the white marlin.

The length-weight relationship by sex was determined for white marlin taken in the gulf from 1971 through 1976 (Figure 4) and in the Atlantic from 1972 through 1976 (Figure 5). Analysis of covariance (Table 2) indicated that length-weight regression coefficients were significantly different between gulf females and males ($F = 16.0$; df = 1, 900; $P<0.001$), gulf males and Atlantic males ($F = 19.2$; df = 1, 514; $P<0.001$), and gulf females and Atlantic females ($F = 10.8$; df = 1, 871; $P<0.001$). The adjusted means were also significantly different between Atlantic females and males ($F = 13.4$; df = 1, 486; $P<0.001$). These findings agree with those of Lenarz and Nakamura (1974), who found a significant difference between sexes in the relationship between weight and eye-fork length for white marlin from the gulf during 1971.

Analysis of covariance was conducted for the length-weight relationship, on a monthly basis, for which sufficient samples were available: gulf females versus Atlantic females in May, June, August, and September, and gulf males versus Atlantic males for June, August, and September. A significant difference in the regression coefficients was found only for the August males ($F = 13.7$; df = 1, 211; $P<0.001$). A significant difference in adjusted means was found for females during June ($F = 9.3$; df = 1, 74; $P<0.005$) and August ($F = 12.0$ df = 1, 286; $P<0.001$), and for males during September ($P = 7.6$; df = 1, 73; $P<0.01$).

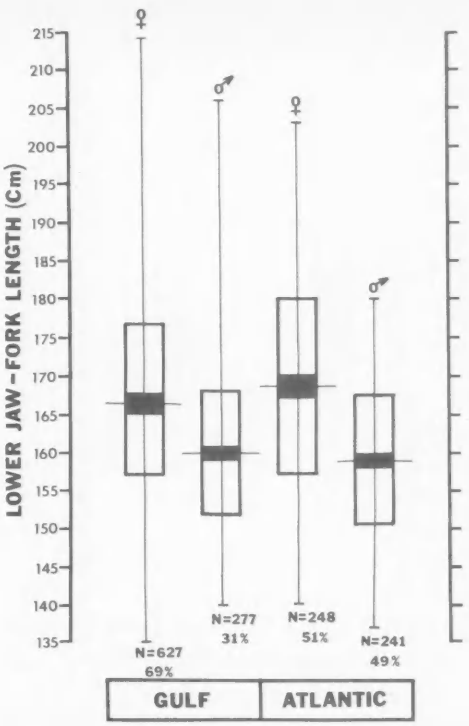

FIGURE 1.—Comparison of length between female and male white marlin collected in the northern Gulf of Mexico (1971 through 1976) and in the Atlantic (1972 through 1976). The number, percent, mean (horizontal line), range (vertical line), 1 SD on each side of the mean (open box), and 2 SE on each side of the mean (shaded box) are shown.

Differences between length-weight relationships of white marlin from the gulf and the Atlantic suggest the possibility of separate groups inhabiting the two areas. Tag returns, however, showed there is at least some migratory movement from the Middle Atlantic Bight to the gulf. To date, tag return data have not shown white marlin migrations in the reverse direction, although one fish tagged in the gulf was recaptured off Cuba, giving some support to the likelihood that they do migrate in the opposite direction (Chester C. Buchanan, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149, pers. commun.)

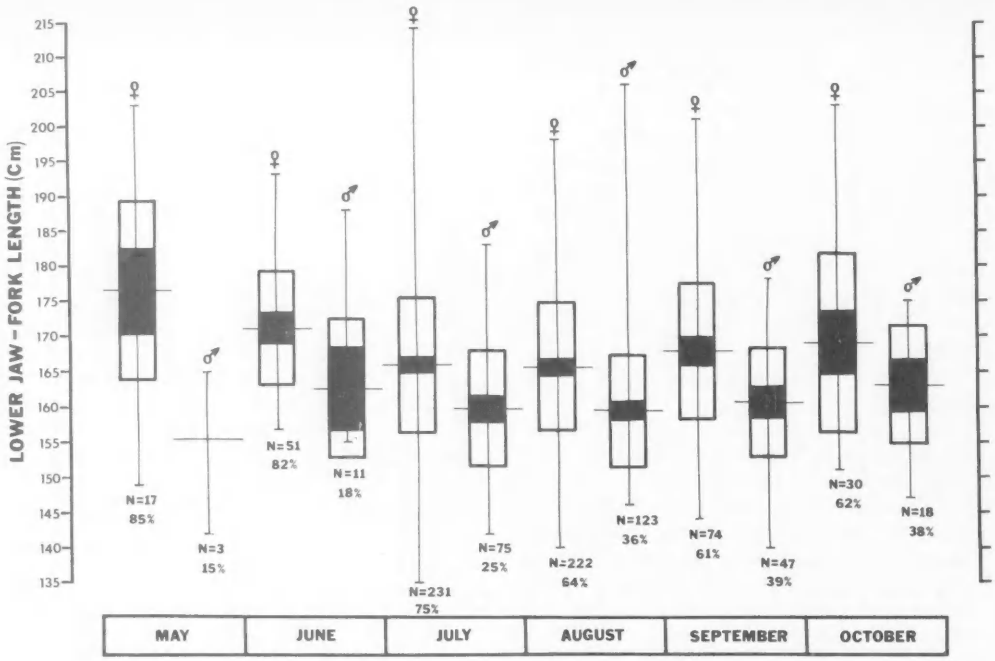

FIGURE 2.—Monthly comparisons of length between female and male white marlin collected in the northern Gulf of Mexico during 1971 through 1976. The number, percent, mean (horizontal line), range (vertical line), 1 SD on each side of the mean (open box), and 2 SE on each side of the mean (shaded box) are shown.

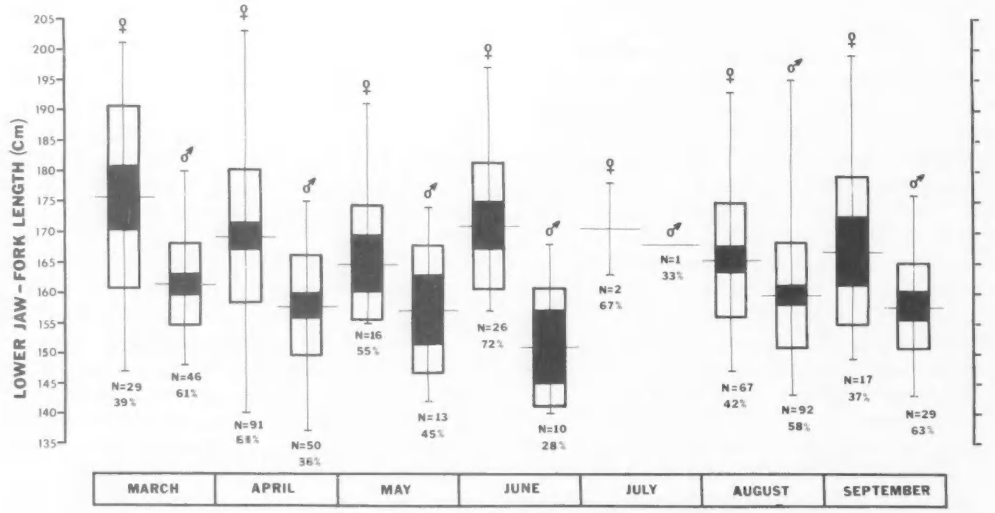

FIGURE 3.—Monthly comparisons of length between female and male white marlin collected in the Atlantic during 1972 through 1976. The number, percent, mean (horizontal line), range (vertical line), 1 SD on each side of the mean (open box), and 2 SE on each side of the mean (shaded box) are shown.

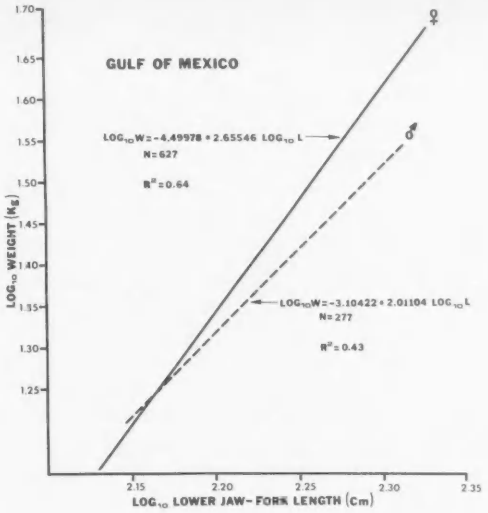

FIGURE 4.—Length-weight relationship (log transformation) for female and male white marlin from the northern Gulf of Mexico.

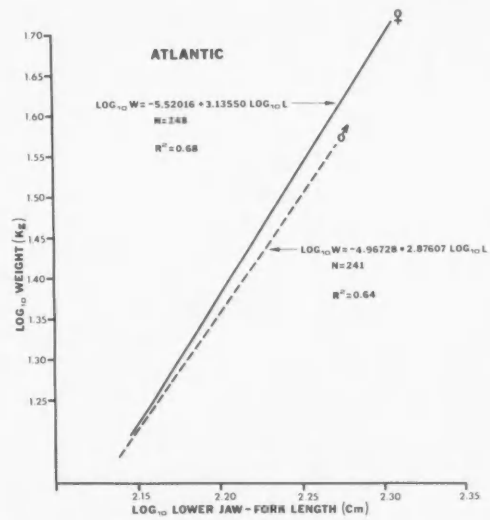

FIGURE 5.—Length-weight relationship (log transformation) for female and male white marlin from the Atlantic.

TABLE 2.—Regression equations, number, sum of squares of x, and mean square calculated for the length-weight relationship ($\log_{10}$ transformations) of white marlin from the northern Gulf of Mexico and the Atlantic.

$Y = \overline{Y} + b(X - \overline{X})$	N	Σx^2	$\frac{\Sigma y^2 - b\Sigma xy}{N-2}$
Gulf and Atlantic females:			
1.41704 + 2.88186(X − 2.22302)	875	0.604832	0.00336706
Gulf and Atlantic males:			
1.34355 + 2.37655(X − 2.20228)	518	0.254956	0.00299720
Gulf females:			
1.39996 + 2.65546(X − 2.22174)	627	0.396458	0.00252756
Gulf males:			
1.32735 + 2.01104(X − 2.20363)	277	0.128593	0.00250737
Atlantic females:			
1.46021 + 3.13550(X − 2.22624)	248	0.204773	0.00377638
Atlantic males:			
1.36217 + 2.87607(X − 2.20073)	241	0.125280	0.00244554
May gulf females:			
1.48714 + 2.60014(X − 2.24572)	17	0.0164014	0.00365206
May Atlantic females:			
1.44276 + 2.96929(X − 2.21669)	16	0.0085322	0.00226977
June gulf females:			
1.44221 + 3.22066(X − 2.23317)	51	0.0210122	0.00162473
June Atlantic females:			
1.40502 + 2.60180(X − 2.23216)	26	0.0163375	0.00323226
June gulf males:			
1.35686 + 3.55091(X − 2.21054)	11	0.00624798	0.00085387
June Atlantic males:			
1.24868 + 3.01101(X − 2.17815)	10	0.00707686	0.00165193
August gulf females:			
1.38976 + 2.72170(X − 2.21831)	222	0.121132	0.00226799
August Atlantic females:			
1.41118 + 2.81615(X − 2.21783)	67	0.0391569	0.00206003
August gulf males:			
1.32575 + 1.93866(X − 2.20207)	123	0.524543	0.00179221
August Atlantic males:			
1.35384 + 2.91546(X − 2.20279)	92	0.0484607	0.00169370
September gulf females:			
1.40689 + 3.01922(X − 2.22399)	74	0.0440863	0.00317564
September Atlantic females:			
1.42732 + 3.10221(X − 2.22137)	17	0.0150308	0.00160237
September gulf males:			
1.32709 + 1.39787(X − 2.20530)	47	0.0199974	0.00220416
September Atlantic males:			
1.34390 + 2.01746(X − 2.19767)	29	0.0105484	0.00144724

Reproduction

A significant difference in egg diameter was found among the anterior, middle, and posterior sections of an ovary from a mature fish ($F = 7.7$; df = 2, 2,676; $P<0.001$). There was no significant difference in mean diameter among the center, midregion, and periphery within each of the three sections. Because some heterogeneity occurred, estimates of fecundity were based, when possible, on eggs from each section of both ovaries. Heterogeneity of egg size within an ovary has also been shown for albacore, *Thunnus alalunga* (Otsu and Uchida 1959), and swordfish, *Xiphias gladius* (Uchiyama and Shomura 1974).

The left ovary ($\overline{X}$ = 25.0 cm, $S_{\overline{X}}$ = 0.732) was significantly longer (F = 35.7; df = 1, 196; $P<0.001$) than the right ovary ($\overline{X}$ = 19.4 cm, $S_{\overline{X}}$ = 0.561). Eldridge and Wares (1974) reported differential growth in the size of ovaries for striped marlin, *Tetrapturus audax*, and for sailfish, *Istiophorus platypterus*. Both were similar to the white marlin in having larger left ovaries.

Well-developed ovaries were present only in 12 white marlin collected during April and May in the Florida Straits. These fish had a GSI of about

6% or greater and were used for estimating fecundity. The mean GSI showed that ovarian weights were lowest during October and increased from November through May (Figure 6). The mean GSI of 2.6 for April and May is lower than the 4.5 mean GSI found by Krumholz (1958) for late April. The GSI of 9.3 (Table 3) agrees with the highest GSI of 9.76 found by Krumholz. The high mean GSI values determined by me for April and May, with the sudden decrease in June, indicated that spawning probably occurred during April and May (Figure 6). Therefore, only one spawning season per year was indicated for the Florida Straits.

White marlin may also spawn in other areas. One fish captured in April 1976 in the Windward Passage had ripe eggs measuring 1.16 mm. Hayasi et al. (1970) found white marlin with mature gonads during April-June in the northern Caribbean. Erdman (1956) found well-developed ovaries in white marlin caught off Puerto Rico in April and found well-formed eggs in a fish taken in June from the same locality.

The smallest fish approaching a ripe condition with large ovaries weighed 26.8 kg (Table 3). Ueyanagi et al. (1970) reported that white marlin reach sexual maturity at 130 cm eye-fork length. Using the conversion equation of Lenarz and Nakamura (1974), 130 cm eye-fork length would be equal to about 20.3 kg.

Frequency distributions of white marlin ovum diameters were made from measurements on 3,912 ova from spent, partly spent, and mature fish (Figure 7). Spent fish caught during May and June contained mostly eggs 0.15 mm in diameter and smaller. Eggs from a partly spent fish caught during June had a frequency mode of about 0.35 mm, with few eggs larger than 0.60 mm. Some of the larger eggs appeared to be undergoing absorption. Jolley (1977), in his histological examination of spent sailfish, found degeneration and absorption of advanced unovulated eggs common. Merrett (1970), studying several species of billfish from the Indian Ocean, suggested that there also may be at least a partial resorption of resting

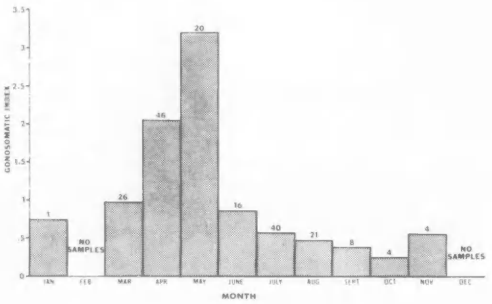

FIGURE 6.—Seasonal variation of mean gonosomatic index in 186 white marlin collected from 1972 to 1976 (number of fish indicated above histograms).

TABLE 3.—Weight, length, and gonadal data for 12 female white marlin from the Florida Straits collected during 1972, 1974, and 1975. The mean and standard error of the mean are given at the bottom of the columns.

Body weight (kg)	Body length (cm)	Ovary wet weight (g)	Gonosomatic index	Estimated number of eggs >0.55 mm in diameter (millions)	Estimated number of eggs >0.29 mm in diameter[1] (millions)
26.8	160	[2]1,600	6.0	5.4	10.4
26.8	169	[2]2,050	7.6	4.8	8.0
30.4	168	[2]2,324	7.6	7.0	11.7
30.4	176	[2]1,700	5.6	3.8	7.3
31.3	168	2,908	9.3	10.4	18.6
32.7	166	2,150	6.6	7.1	11.8
32.7	166	2,693	8.2	10.1	16.8
33.6	167	2,161	6.4	7.6	11.9
35.0	169	[2]2,250	6.4	6.5	10.2
35.4	170	[2]2,320	6.6	7.5	14.4
36.3	171	2,488	6.8	10.5	20.2
37.2	179	[2]2,050	5.5	8.1	14.5
32.4	169	2,224	6.9	7.4	13.0
0.98	1.4	107	0.32	0.62	1.16

[1]Estimated using actual percent from 0.30 to 0.55 mm in diameter from 25 eggs measured for each fish.
[2]Entire ovaries available.

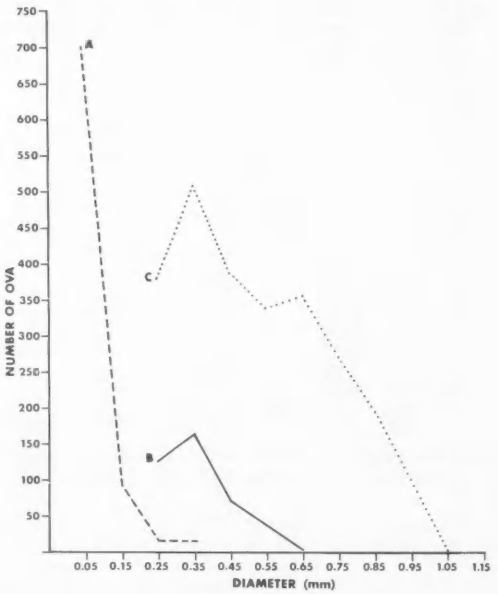

FIGURE 7.—Frequency distribution of white marlin ovum diameters for: A, four spent fish (827 ova) in May and June; B, one partially spent fish (406 ova) in June; C, one mature fish (2, 679 ova) in April.

oocytes. I found frequency modes of about 0.35 mm and 0.65 mm in a mature fish caught in April. Only eggs measuring 0.56 mm and larger were included when estimating fecundity. Because there were two frequency modes present in mature fish, an estimate of the number of eggs 0.30 mm in diameter and larger is also presented (Table 3).

Fecundity, based on the number of ova in the most advanced size mode, ranged from 3.8 to 10.5 million eggs ($\bar{X} = 7.4, S_{\bar{X}} = 0.62$) for white marlin weighing 26.8 to 37.2 kg (Table 3). The number of mature ova per gram of body weight ranged from 125 to 332 ($\bar{X} = 227, S_{\bar{X}} = 16.76$). The average number of eggs measuring 0.30 mm in diameter and larger was estimated as 13 million ($S_{\bar{X}} = 1.16$).

Fecundity was based on the number of fully yolked eggs, forming a group distinct from another group of developing eggs. Fecundity would vary depending on whether smaller eggs develop further or are absorbed. If fractional spawning occurs, as reported for sailfish by Jolley (1977), the eggs in the next distinct group should be included in seasonal fecundity estimates.

Acknowledgments

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RECORDS OF PISCIVORUS LEECHES (HIRUDINEA) FROM THE CENTRAL COLUMBIA RIVER, WASHINGTON STATE

No records of leech infestations on fish of the Columbia River exist in the published literature. As a whole, the freshwater hirudinean fauna of the Pacific Northwest remains a relatively unsurveyed, little known, and neglected biotic group. This is due, in part, to problems in leech identification as well as in obtaining representative collections.

We obtained leeches from the external surface, oral cavity, and gill chambers of fish during a continuing environmental assessment program on the central Columbia River above Richland, Wash. (Benton and Franklin Counties), from 1975 through 1977. This paper identifies four piscivorous species, provides new host and distribution records, and reviews some recent taxonomic changes for the species encountered. Ecological observations are included.

The leeches recorded herein are *Myzobdella lugubris* Leidy 1851, *Piscicola salmositica* Meyer 1946, *Placobdella montifera* Moore 1906, and *Actinobdella inequiannulata* Moore 1901.

Methods and Site Description

Fish were collected at monthly or bimonthly intervals by a variety of gear (gill nets, trammel nets, hoop nets, beach seines, and electroshocker) from January 1975 to December 1977. Over 20,000 fish, representing nearly 40 species, were examined during this period (Gray and Dauble 1977). Leech specimens were preserved in 10% Formalin[1] solution, either when captured or after being examined alive in the laboratory.

Our leech collections were more qualitative than quantitative because leech-fish associations in nature are normally periodic and facultative despite the nutritional requirement of piscivorous leeches for fish blood. Also, piscivorous leeches can readily detach from fish captured by most types of fishing gear, particularly from fish recovered when moribund or dead.

Occurrence of many freshwater leech species can be correlated with characteristic aquatic habitats. Water quality parameters vary seasonally in the central Columbia River, as follows: dissolved oxygen, 8.0-12.0 mg/l; pH, 7.4-8.6; phosphate (as PO_4), 0.03-0.04 mg/l; ammonia-nitrogen, 0.01-0.2 mg/l; hardness (Ca, Mg), 55-75 mg/l; and alkalinity ($CaCO_3$), 50-67 mg/l. Water temperatures range from 1° to 3°C in midwinter to about 21°C in late August and early September. There are no significant quantities of organic and inorganic pollutants (our data). The water carries minimal silt loads.

The central Columbia River in the Hanford Reach where our collections were made (river km 550-629) survives as the last free-flowing section of the main channel above Bonneville Dam. Decades of hydroelectric development have transformed other sections into a consecutive series of river-run reservoirs. River flows in the study area usually range from about 2,000 m^3/s over much of the year to over 12,000 m^3/s during the annual spring spate, when surplus runoff is passed downriver over spillways from reservoirs (Nees and Corley[2]).

Additionally, Hanford flows are now regulated at Priest Rapids Dam in response to daily and weekly power demand peaks, causing water levels in the river to fluctuate widely. This periodically exposes and inundates a rocky or muddy shoreline zone, apparently restricting development of a diverse leech fauna along the river margins. Water levels in Wanapum Reservoir behind Priest Rapids Dam (river km 639) and in Umatilla Reservoir behind McNary Dam (river km 470) are relatively stable, although subject to controlled summer drawdowns. Substantial populations of such common omnivorous leeches as *Erpobdella punctata* (Leidy 1870), *Helobdella stagnalis* (Linnaeus 1758), and *Theromyzon* spp. occur along the

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[2]Nees, W. L., and J. P. Corley. 1974. Environmental surveillance at Hanford for CY-1973. Unpubl. manuscr., 56 p. R&D Rep., BNWL-1881, Battelle, Pacific Northwest Laboratories, Richland, WA 99352.

margins of these mid-Columbia River reservoirs (our observations).

Results and Discussion

Four leech species were recovered from Columbia River fish (Table 1). About 90% of the specimens were *Myzobdella lugubris*. Two families belonging to the order Rhynchobdella were represented, Glossiphoniidae and Piscicolidae. Members of this order typically possess a small pore on the anterior sucker for a mouth, from which a muscular pharyngeal proboscis can be protruded, and lack biting jaws or denticles. Relatively few glossiphoniids are piscivorous (Klemm 1975). However, the piscicolids characteristically are ectoparasites of fish and feed on fish blood. The muscular proboscis of piscicolids is effective in penetrating epidermal layers of fish wherever scales are reduced or absent, although gills are favored feeding sites.

Myzobdella lugubris

Myzobdella lugubris has not been recorded previously as a common ectoparasite of Columbia River fish. Its distribution and host records are included in previous publications that refer to the genus *Illinobdella* in which *M. lugubris* was formerly placed.

Myzobdella lugubris and *M.* (syn. *Illinobdella*) *moorei* (Meyer and Moore 1954) were until recently believed to be two distinct species. The former was considered characteristic of brackish and marine waters, while the latter was considered characteristic of freshwater. The distinction was primarily ecological since anatomical features of both species were remarkably similar. However, *M. lugubris* and *M. moorei* are now considered to be a single euryhaline species (Sawyer et al. 1975).

Further, it now appears that all members of the related piscicolid genus *Illinobdella* are synonymous with *M. lugubris*. Thus species reported in the literature as *Illinobdella alba*, *I. elongata*, and *I. richardsoni*, as well as *M.* (=*I.*) *moorei*, all preying on fish in North American waters (Meyer 1940, 1946b), are junior synonyms of *M. lugubris*, which holds taxonomic priority. Locality and host records of the ubiquitous *M. lugubris* under these synonyms are given by Hoffman (1967), Klemm (1972a, b, 1977), and Sawyer et al. (1975). Studies on *M. lugubris* infesting the blue crab, *Callinectes sapidus*, and the white catfish, *Ictalurus catus*, in a South Carolina tidal river support this synonymy (Daniels and Sawyer 1975).

Myzobdella lugubris was recovered from a wide size range of adult chiselmouth, *Acrocheilus alutaceus*, and northern squawfish, *Ptychocheilus oregonensis*, in our collections, and less frequently from adult suckers, *Catostomus macrocheilus* and *C. columbianus*. The associations were apparently facultative. *Myzobdella lugubris* occurred primarily in the oral cavity of chiselmouth (Figure 1) and northern squawfish, where they were retained during the struggle of hosts captured in overnight net sets. Leeches were recorded and counted the next day when fish were recovered. Many leeches on the external surfaces of moribund or dead fish may have detached before net recovery. *Myzobdella lugubris* were never found in the mouth of suckers but only in the axila of pelvic or pectoral fins, on fin rays, or in the gill chambers.

Myzobdella lugubris was also a fairly common ectoparasite of brown bullhead, *I. nebulosus*, collected by angling in backwater sloughs of the central Columbia and lower Snake Rivers during the summer. Infestations on bullheads usually consisted of one or two small leeches attached to the pectoral or pelvic fins.

The incidence of *M. lugubris* on adult chiselmouth and northern squawfish (Table 2) shows infestations only during June, July, and August when Columbia River water temperatures ranged from 13° to 21°C. The leeches were primarily sexually mature. Collections from the oral cavity of chiselmouth in October 1975, 1977 and November 1977 contained numerous small, immature leeches that had apparently hatched within the preceding 1 or 2 mo.

TABLE 1.—Piscivorous leeches (Hirudinea) collected in this survey from teleost fishes in the central Columbia River, Washington State.

Species	Host infected
Piscicolidae:	
Myzobdella lugubris	Northern squawfish, *Ptychocheilus oregonensis*
	Chiselmouth, *Acrocheilus alutaceus*
	Brown bullhead, *Ictalurus nebulosus*
	Largescale sucker, *Catostomus macrocheilus*
	Bridgelip sucker, *C. columbianus*
Piscicola salmositica	Chinook salmon, *Oncorhynchus tshawytscha*, fry
	Sucker, *Catostomus* sp., fingerling
Glossiphoniidae:	
Placobdella montifera	Sucker, *Catostomus* sp., fingerling
Actinobdella inequiannulata	Largescale sucker, *C. macrocheilus*

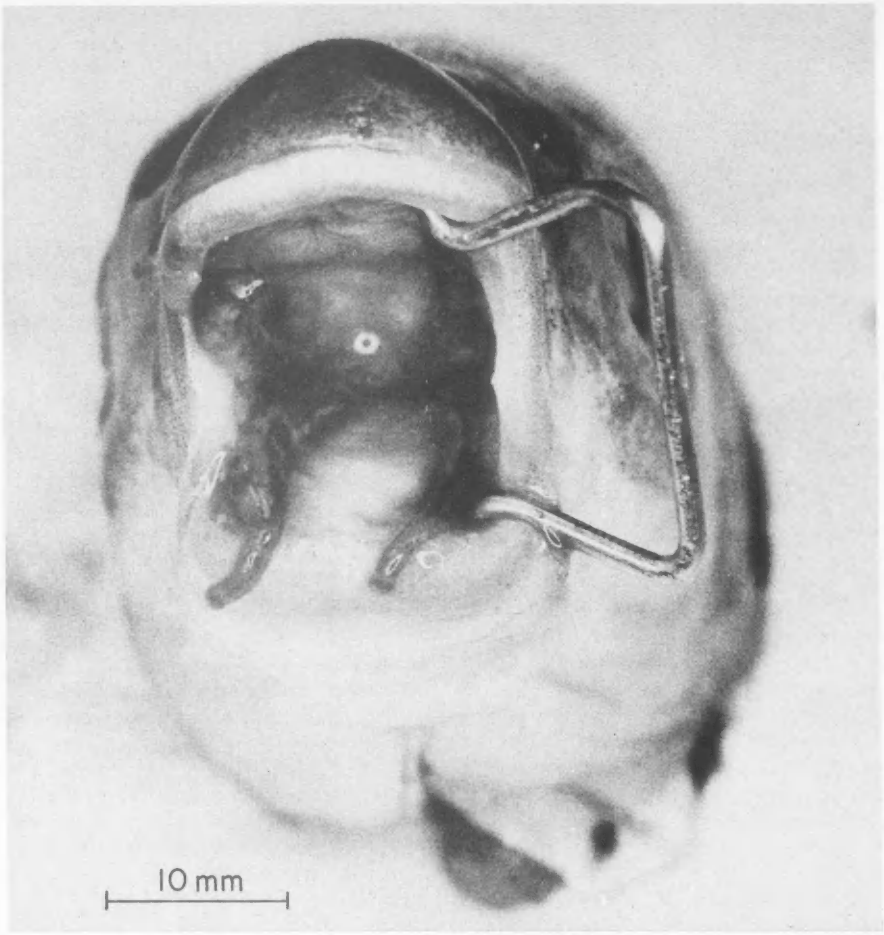

FIGURE 1.—Four sexually mature *Myzobdella lugubris* in the oral cavity of chiselmouth collected in the central Columbia River. The small subterminal mouth of the host is bordered by a cartilaginous upper and lower lip for grazing on sessile algae. The leeches occupy most of the available space in the oral cavity when the mouth is closed.

TABLE 2.—Incidence of infestation of chiselmouth and northern squawfish by the piscicolid leech, *Myzobdella lugubris*, indicated by infestation ratio.[1]

Month	Chiselmouth			Northern squawfish		
	1975	1976	1977	1975	1976	1977
Jan.	0/5	0/4	—	0/5	0/2	0/1
Feb.	0/1	—	—	0/3	0/2	0/1
Mar.	—	—	—	0/1	—	—
Apr.	0/5	0/3	0/4	0/14	0/9	0/7
May	0/22	0/5	0/10	0/34	0/7	0/14
June	0/32	0/16	6/27	0/33	0/3	0/19
July	1/32	8/19	1/12	3/38	0/16	6/25
Aug.	1/19	0/4	19/42	0/13	0/2	0/8
Sept.	0/46	0/9	0/13	0/18	0/15	0/4
Oct.	[2]7/37	0/10	[2]3/13	0/23	0/2	0/1
Nov.	0/7	0/2	[2]7/9	0/4	—	0/3
Dec.	0/6	0/7	0/2	0/2	—	0/1

[1]Infestation ratio = number of fish infested/number of fish examined.
[2]Numerous small leeches, recently hatched, were attached to some hosts.

According to Sawyer et al. (1975), *M. lugubris* is a relatively warm-water species encountered most often at 21°-30°C, occasionally at 16°-20°C, and less often in colder water. They reported that the leech appeared to be injured if the water was suddenly cooled to 10°-15°C in laboratory experiments. Obviously some *M. lugubris* survive over winter at low temperatures, but it must remain inconspicuous due to dormancy in temperate regions of North America. We have never recovered *M. lugubris* during winter in the central Columbia River, either from fish or from benthic samples

designed to quantitatively collect invertebrates.

Large, adult *M. lugubris* from Columbia River fish were characterized by a green background coloration, superficially suggesting that they fed on algal cells ingested by the host. Chiselmouth and suckers commonly feed on sessile, green-colored diatoms from bottom substrates. However, microscopic examination revealed that this coloration was due entirely to pigments in the adult leech's musculature and not to the presence of algae in their digestive tract. *Myzobdella lugubris* fed entirely on fish blood cells and plasma.

Feeding on fish blood is clearly required by *M. lugubris* for growth and reproduction. Copulating *M. lugubris* were noted on fish. But since deposition of a cocoon requires hard substrates, sexually mature leeches must eventually detach, thus freeing fish of infestations. The breeding, growth, and reproductive cycle of piscivorous leeches may account for the periodic infestations of fish so frequently documented in the literature.

In the Columbia River, the cycle in *M. lugubris* is correlated with a seasonal change in water temperatures, with peak activity occurring in late summer and fall.

In tidal estuaries on the east coast of the United States, *M. lugubris* has a life cycle that involves two hosts, a fish and a crustacean. It engorges on fish blood before detaching to deposit cocoons on crabs (Daniels and Sawyer 1975). This indicates possible involvement of a freshwater crustacean in the life cycle of *M. lugubris* in the Columbia River. The only large crustacean available is *Pacifasticus leniusculus*, but extensive collections of this crawfish in previous years by the senior author disclosed no attached leeches. Therefore, stones are probably used as cocoon deposition sites in the Columbia River.

Piscivorous leeches are often vectors of hemoflagellates (genera *Trypanoplasma* and *Trypanosoma*) found in the blood of freshwater and marine fishes (Khaibulaev 1970; Becker 1977). Although we have occasionally detected *Trypanoplasma* in Columbia River fish, we found no hemoflagellates in the digestive tract of over 20 *M. lugubris* taken from various hosts.

We did not examine histopathology of leech attachment and feeding sites in the oral cavity of infested Columbia River fish, although petechiae were evident during the fall on some chiselmouth. Inflammatory conditions and hyperplasia were described previously from a massive infestation of *M. lugubris* (misidentified as *Cystobranchus virginicus*) on white catfish in Virginia (Paperna and Zwerner 1974).

Piscicola salmositica

The salmonid leech, *P. salmositica*, was described from specimens taken, in part, from sea-run steelhead trout, *Salmo gairdneri*, transferred from the Columbia River to Mason Creek, Chelan County, Wash. (Meyer 1946a). The leeches infesting the fish originated either in the Columbia River or from Mason Creek. Thus the salmonid leech has previously been recorded from the upper Columbia River system. This species is usually associated with fall spawning runs of adult salmonid fishes in coastal streams, but it occurs elsewhere in the Pacific Northwest (Becker and Katz 1965a).

We collected several *P. salmositica* at various times from chinook salmon, *Oncorhynchus tshawytscha*, fry and once from a fingerling sucker. Each infestation consisted of a solitary leech attached to the dorsal surface of its host and feeding on blood. All specimens were taken in April and June as water temperatures (10°-14°C) increased and consisted of small leeches that presumably had hatched from cocoons the previous fall or winter. Three specimens contained developing trypanoplasms among their intestinal contents, evidence of prior feeding on infected fish. Therefore, *P. salmositica* is confirmed as a vector transmitting trypanoplasms among various fish in the central Columbia River. The salmonid leech is the only known vector of the piscine hemoflagellate *Trypanoplasma salmositica* (Katz 1951) in the Pacific Northwest (Becker and Katz 1965b).

Piscicola salmositica requires meals of fish blood before detaching to deposit cocoons on bottom substrates (Becker and Katz 1965a). Thus salmonid leeches presumably occur among and infest populations of anadromous chinook salmon that spawn each fall in the central Columbia River near our fish collection sites. However, we have not detected *P. salmositica* on transient adult fall chinook salmon returning from the sea to spawn or from downstream drifting, spawned out salmon carcasses. Neither have we found salmonid leeches on several adult steelhead trout and spring-run chinook salmon examined during the summer at the Ringold Hatchery (Washington State Department of Game) above Richland. On the basis of our observations, *P. salmositica* is not an abundant leech in the central Columbia River.

Placobdella montifera

One immature *P. montifera* was recovered from the dorsal surface of a fingerling sucker in early October 1976. We also collected one adult specimen from beneath shoreline rocks at Umatilla Reservoir during June where it was depositing a cocoon. The species is not a common ectoparasite of fish. It probably occurs mostly along reservoir shorelines where water levels remain relatively stable, rather than along the margins of the free-flowing Columbia River above Richland.

Placobdella montifera has been reported to attack aquatic worms, insect larvae, mussels, frogs, toads, and fish, but the only specific host records are fish (Hoffman 1967; Klemm 1972a, 1975, 1976; Sawyer 1972; and others). This leech, as do most glossiphoniids, broods its cocoon and carries its young. An uncommon but widely distributed species, *P. montifera* is listed as having been reported previously from Washington (Klemm 1972b). Distributional records probably valid include British Columbia, Saskatchewan, Ontario, and the northern states east of the Mississippi River southward to Georgia (Sawyer 1972; Klemm 1977).

Actinobdella inequiannulata

Six *A. inequiannulata* were collected from the axila of the pelvic and pectoral fins of one adult largescale sucker in mid-August 1975. According to Sawyer (1972), this glossiphoniid is known from Illinois, Minnesota, and Ohio; Klemm (1972a, b, 1977) adds Michigan, Pennsylvania, and New York; and Daniels and Freeman (1976) add Ontario. *Actinobdella triannulata* Moore 1924, a name common in earlier literature, is now considered a junior synonym of *A. inequiannulata* (Daniels and Freeman 1976; Klemm 1977).

Daniels and Freeman (1976) provide a redescription of *A. inequiannulata* on basis of specimens collected from two species of suckers (genus *Catostomus*) and preserved material from the U.S. National Museum. The species was earlier considered as free-living with no known hosts (Sawyer 1972; Klemm 1972a). Since its synonym *A. triannulata* displayed a predilection for suckers (Hoffman 1967), the host preference of *A. inequiannulata* is now partially resolved. Little is known of its ecology and life cycle. We did not examine our specimens for ingested fish blood.

The host relationship for glossiphoniids is generally considered to be less obligatory than for piscicolids, and most are omnivorous feeders. Apparently *A. inequiannulata*, *P. montifera*, and *P. pediculata* Hemingway 1908 are the only three American glossiphoniids consistently reported to parasitize fish. Several authors have reported *P. pediculata* from the freshwater drum, *Aplodinotus grunniens*, and Sawyer (1972) has indicated a high degree of host specificity; it has not been reported from the Pacific Northwest, nor would it be expected in this region due to its narrow host preference.

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INDUCED SPAWNING AND LARVAL REARING OF THE YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA*

The yellowtail flounder, *Limanda ferruginea* (Storer), a commercially important flatfish, occurs in North American continental waters from the north shore of the Gulf of St. Lawrence southward to the lower part of Chesapeake Bay (Bigelow and Schroeder 1953). The yellowtail flounder spawns from March through August where water temperatures over its range vary from about 5° to 12°C (Colton 1972). The eggs are pelagic and lack an oil globule; diameter of the live eggs (range 0.79-1.01 mm) averages 0.88 mm (Colton and Marak 1969).

A program to obtain viable yellowtail eggs through hormone induction, to rear larvae through metamorphosis, and to determine the mechanisms of survival of early life stages under controlled laboratory conditions was undertaken. The successful induction of yellowtail flounder and subsequent rearing of the larvae through metamorphosis marks the first time the early life history of this flatfish has been completed in the laboratory.

Materials and Methods

Adult yellowtail flounder were captured by otter trawling in Block Island Sound in the winters of 1974, 1975, and 1976 and transported to the Narragansett Laboratory in a 380-l live car equipped with an aerator. In the laboratory the fish were held in a 28,000-l aquarium. A continual supply of filtered seawater was pumped to the aquarium from Narragansett Bay.

Individuals presumed to be sexually mature were selected by length. Available length-weight data (Lux 1969) indicated that yellowtail flounder in southern New England waters mature when they attain a length near 35 cm or an age of 3 yr (Lux and Nichy 1969). After acclimating in the laboratory, the fish were segregated by sex, measured and weighed, and tagged with numbered plastic pennants secured through the caudal peduncle. Yellowtail flounder were sexed by holding the white underside to the light and looking through the flesh. The outline of the ovary extending posteriorly from the mass of viscera can readily be seen even in immature females (Royce et al. 1959). Yellowtail flounder are delicate and excitable. To minimize injury, the fish were anesthetized in a solution of tricane methanesulfonate (MS-222[1]) at a concentration of 1:20,000 (Leitritz and Lewis 1976) during each examination.

While the fish were held in captivity, a photoperiod of 11 h of light and 13 h of dark simulated spawning light conditions. Four banks of fluorescent lights (each bank composed of 16 40-W bulbs) were suspended 4 m from the ceiling and mechanically timed. The light banks were sequentially turned on and off in the morning and evening at 15-min intervals to simulate dawn and twilight. Prior to receiving hormones the fish were fed a daily diet of chopped frozen hake, whiting, or squid. During the trials the fish were not fed.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The effectiveness of the pituitary preparations was evaluated by monitoring the gonosomatic index (GSI), ovulation, success of egg fertilization, and hatching success. Hormones were prepared on the day of injection, and dosages were established by the weight of each individual fish. A saline solution of isotonic sodium chloride was used as a carrier. All injections were administered (2-cm^3 syringe, 20 gage 3.85-cm needle) intramuscularly into the back below the dorsal fin. Inserting and withdrawing the needle slowly aided in retaining most of the fluid in the flesh. After injection, the flesh of the fish was massaged to diffuse the fluid into the muscles.

Sexually mature fish were hand stripped and the eggs fertilized in a polyethylene pan. Several thousand eggs were collected at each spawning, and the sperm of two males was used to fertilize the eggs from each female. Yellowtail flounder are nonsynchronous spawners (Bigelow and Schroeder 1953), and multiple spawnings occurred among most induced fish. The fecundity of yellowtail flounder increases with age and body length, and an individual female may yield from 350,000 to more than 4,000,000 eggs during the spawning season (Pitt 1971).

The state of ova maturation of the experimental fish was observed at the start and termination of each experiment. Before injecting, a polyethylene cannula was inserted into the oviduct and oocyte samples were orally withdrawn. The oogenesis of oocytes was divided by microscopic observation into three general histological stages:

Stage I - the primary oocyte stage, oocytes contained cytoplasmic vacuoles and measured between 0.1 and 0.25 mm.

Stage II - the yolk globule stage, cytoplasm of oocytes was filled with dense yolk granules and measured up to 0.6 mm.

Stage III - ripe stage, hyaline oocytes present and measured 0.75-1.00 mm in size.

Fertilized eggs were incubated in static, aerated, black-sided aquaria that had been inoculated with the green algae *Dunaliella* sp. A single application of penicillin (25 international units [IU]/ml) and streptomycin (0.02 mg/ml) at the concentration of 50 mg/l was effective in controlling bacterial contamination of the aquaria in almost all cases.

Three series of experiments were undertaken to determine the effectiveness of the hormone injections (Table 1). The first trial was conducted in winter 1975 to determine if induced spawning would occur at low winter water temperatures. The second and third were conducted in the springs of 1976-77 and coincided with the yellowtail flounder's natural spawning season.

Hormone dosage levels of 2, 5, and 10 mg/kg fish and frequency of injecting were dictated by previous successful results obtained with the summer flounder, *Paralichthys dentatus*, (Smigielski 1975a) and winter flounder, *Pseudopleuronectes americanus*, (Smigielski 1975b). After each trial the female fish were killed and reweighed, the ovaries were examined, and gonosomatic indices were recorded. Prior to receiving hormone injections, all the female test fish in the first trial were in Stage I of oocyte oogenesis, and most females prior to the second and third trials were in Stage II. Males were not injected in the second and third trials because they were sexually ripe.

Results and Discussion

First Trial

In the first trial (Table 1), most females in the group receiving 10 daily injections of 2 mg pituitary were refractory with low GSI values (7-13%). One fish hydrated but did not ovulate, and a small number of Stage II ova were found in the ovaries. Hydration is an increase in total body weight. The weight gain is due mostly to water intake and is reflected by higher GSI values as most of the water appears to go into the gonads. Excessive hydration is manifested by grossly bloated fish which in some instances can hydrate to the point of death without ovulating.

TABLE 1.—Hormone dosages, water temperatures, and number of yellowtail flounder in each trial.

	Trial 1 - January 1975 Water temperatures, 3°-6°C (Mean 5.1°C)			Trial 2 - April 1976 Water temperatures, 7°-10°C (Mean 9.2°C)			Trial 3 - April 1977 Water temperatures, 8.5°-12.5°C (Mean 10.1°C)		
Daily carp pituitary dosages	Number of females	Number of males	Uninjected controls	Number of females	Number of males	Sham injected controls	Number of females	Number of males	Sham injected controls
2.0 mg/kg fish	6	4	3	8	0	4	9	0	4
5.0 mg/kg fish	6	4	3	8	0	4			
10.0 mg/kg fish	6	4	3	7	0	4			

In the group of females receiving 10 daily injections of 5 mg, three fish were refractory with low GSI values (10-15%), and three hydrated but did not ovulate. Two of the latter fish contained a small number of Stage II ova; the other developed a cloacal plug of membranous tissue and Stage I ova.

In the group receiving 10 daily injections of 10 mg, all were refractory with low GSI values (9-11%), except for one fish that hydrated but did not ovulate. A membranous plug developed in the cloaca of this fish, and it was bloated. A very small number of Stage II ova were found in the ovaries. There was no indication of sexual ripening in the uninjected control fish, and their GSI values were low (10-13%). Copious semen was obtained from the males injected at all three dosages; however, fertilization was not attempted. It was reasoned from the first trial that low GSI values (7-15%) of females coupled with low water temperatures (3°-6°C, mean 5.1°C) that were less than optimum inhibited the effectiveness of the hormones, for although some fish hydrated, they did not ovulate.

Second Trial

The results obtained from the second trial were variable (Table 2). All but one fish receiving injections of 2 mg hydrated and ovulated. Two fish died during the trial; one, after yielding spawn on two occasions, developed a membranous plug and became grossly bloated.

In the group receiving injections of 5 mg, two fish ovulated but the eggs obtained were not fertile. Three other fish developed plugs and hydrated to the point of death. Injections were discontinued at the first sign of abnormal hydration, but the fish continued to imbibe water.

In the group that received 10 mg, five fish experienced excessive hydration manifestated by bloating, plug formation, and, in two instances, death. The membranous plugs were identical to those that developed in the test group that received hormone dosages of 5 mg. The controls had four fish with signs of hydration but no Stage III ova were found in their ovaries.

Third Trial

The results of the third trial paralleled those of the second trial at a dosage of 2 mg. Seven of the experimental females hydrated normally and ovulated (Table 3). Fertilization and hatching of these eggs were satisfactory and the larvae were normal. The remaining two fish died during the trial, and their ovaries had a small number of Stage III ova. The control fish neither hydrated nor ovulated; GSI values were fairly high, but Stage III ova were absent.

The anomalous hydration with bloating and formation of membranous plugs during hormonal induction is not unique. Clemens and Grant (1964) injected female goldfish, *Carassius auratus*, with carp pituitary and observed that the gonadal water content increased, apparently in association with ovulation. The hormone regulating the hydration process appeared to be a gonadotropin.

Shehadeh and Ellis (1970) reported the formation of plugs in the cloaca in striped mullet, *Mugil cephalus*, treated with a combination of salmon pituitary and Synahorin. Sinha (1971) studied the gonadal hydration response of *Puntis gonionotus* using the second fraction of molecular seived carp pituitary extract and suggested that the second fraction is involved in osmoregulation, since an injection of an additional amount enhances the rate of water transport resulting in maturation.

Hirose and Ishida (1974) studied the effects of Cortisol and human chorionic gonadotropin (HCG) in ayu, *Plecoglossus altivelis*, and reported that the water content of the ovary from hormone-treated fish increased by 6%. Smigielski (1975b) reported a similar response in winter flounder injected with pregnant mare serum (PMS) and HCG. Hirose (1976) demonstrated that gonadotropin-treated ayu imbided a greater quantity of water than control ayu. He suggested that gonadotropin may act on the sodium and potassium system or permeability of the egg membrane.

Hydration is a normal and necessary prelude to maturation and ovulation. The cases of abnormal hydration experienced with yellowtail flounder may be attributed to an adverse reaction to hormone dosage. Most of the test fish that hydrated abnormally and became bloated had an increase in body weight of more than 10%. The increase in body weight appeared to be a result of the fish imbibing an excess amount of water. An excessive amount of introduced hormone may upset the water transport or sodium potassium systems, resulting in more water bing imbibed.

In conclusion, it appears that water temperatures higher than 6°C and GSI values approaching 20% coupled with carp pituitary injections approximating 2 mg/kg of fish is an effective combi-

TABLE 2.—Effects of carp pituitary on yellowtail flounder receiving daily injections. All fish were exposed to 11L:13D photoperiod and water temperatures of 8.5°-12.5°C (Mean 10.1°C). Symbols: + = did, 0 = did not hydrate or ovulate.

Dosage	No. of injections	Total length (mm)	Initial body weight (g)	Weight change (% initial wt)	GSI (% final wt)	Effect		Date of spawning 1976	Fertilization (%)	Hatch (%)
						Hydrated	Ovulated			
2.0 mg/kg fish	8	348	396	+6.94	19.7	+[1]	0			
	7	340	392	−1.84	5.6	+	+	Apr. 6	80	70
								Apr. 7	70	75
	4	353	421	−3.30	5.1	+	+	Apr. 6	75	55
								Apr. 7	70	60
								Apr. 8	80	70
								Apr. 9	90	75
								Apr. 11	70	60
	1	435	817	−0.96	4.3	+	+	Apr. 4	75	80
								Apr. 5	80	75
								Apr. 6	70	60
								Apr. 7	70	50
								Apr. 9	75	75
	6	280	263	−0.49	7.0	+	+	Apr. 5	80	75
								Apr. 7	75	70
								Apr. 8	80	70
	4	350	381	+1.12	8.4	+	+	Apr. 8	80	60
								Apr. 9	80	50
								Apr. 11	70	80
	6	450	882	+9.54	24.0	+	+[2]	Apr. 1	80	75
								Apr. 3	75	70
	6	387	721	+0.98	11.2	+	+	Apr. 5	80	80
								Apr. 6	75	65
Controls		420	667	+2.12	18.6	0	0			
		392	611	+2.63	19.6	+	0			
		361	409	+1.09	10.5	0	0			
		381	562	+0.44	9.8	0	0			
5.0 mg/kg fish	5	401	683	+2.11	18.6	+	+[3]			
	6	501	1,489	+9.62	29.5	+[2]	0			
	4	307	566	+11.69	26.1	+[2]	0			
	5	435	1,131	+13.17	24.9	+[2]	0			
	10	348	762	−0.19	4.6	0	0			
	5	351	491	+8.47	30.8	+[4]	+[3]			
	10	336	418	+0.96	11.0	0	0			
Controls		361	521	+2.92	19.3	+	0			
		392	587	+2.87	19.5	+	0			
		406	702	+2.19	15.1	0	0			
		339	367	+1.87	12.9	0	0			
10 mg/kg fish	5	467	1,259	+11.15	28.6	+[4]	0			
	4	346	593	+13.57	27.6	+[2]	0			
	5	352	463	+15.11	29.6	+[4]	+[3]			
	5	433	1,245	+10.76	25.3	+[4]	0			
	7	341	485	+14.06	29.1	+[2]	0			
	10	360	501	+1.16	12.6	0	0			
	10	348	437	+1.84	14.2	0	0			
Controls		343	428	+1.23	15.1	0	0			
		389	672	+2.63	17.9	+	0			
		430	891	+4.78	19.3	+	0			
		369	551	+1.63	14.3	0	0			

[1]Died, ~ 10% Stage III ova in ovaries, not fertilized.
[2]Plug formed, fish became bloated and hydrated to point of death.
[3]Stage III ova in ovaries, not fertilized.
[4]Plug formed, fish became bloated.

nation for inducing spawning of yellowtail flounder.

Larval Rearing

Fertilized yellowtail flounder embryos were incubated in 64-l, rectangular, black-sided, static, well-aerated aquaria at a density of approximately 80 embryos/l. The incubating and rearing temperature was 10°C and the salinity 32‰. Banks of 40-W timed fluorescent lights suspended 1 m over the aquaria simulated a day and night regimen of 15 h light and 9 h dark (15L:9D). The aquaria were inoculated with green algae (*Dunaliella* sp.) which may have aided in the removal of metabolic waste products produced by the larvae. The algae also served to sustain the zooplankton introduced as food. A single application of penicillin (25 IU/ml) and streptomycin (0.02 mg/ml) was effective in controlling bacterial contamination in almost all cases.

At 10°C, hatching occurred 6-7 days after fertilization. Yolk absorption occurred 4-5 days after hatching, which coincided with first feeding. The larvae averaged 2.75 mm long upon hatching and possessed a completely formed gut. The eyes were

TABLE 3.—Effects of carp pituitary on yellowtail flounder receiving daily injections. All fish were exposed to 11L:13D photoperiod and water temperatures of 8.5°-12.5°C (Mean 10.1°C). Symbols: + = did, 0 = did not hydrate or ovulate.

Dosage	No. of injections	Total length (mm)	Initial body weight (g)	Weight change (% initial wt)	GSI (% final wt)	Effect		Date of spawning 1977	Fertilization (%)	Hatch (%)
						Hydrated	Ovulated			
2.0 mg/kg fish	3	391	552	+0.56	4.6	+	+	Apr. 12	75	80
	3	453	898	+9.13	21.2	+[1]	0			
	2	474	1,298	+4.70	6.9	+	+	Apr. 12	80	70
								Apr. 14	80	75
	4	424	878	+7.16	20.8	+[1]	0			
	5	412	733	+2.04	5.3	+	+	Apr. 16	50	60
								Apr. 17	60	40
								Apr. 18	60	45
	5	364	486	+0.97	10.7	+	+	Apr. 17	60	55
								Apr. 18	70	65
	6	396	598	+1.62	8.8	+	+	Apr. 17	70	60
								Apr. 18	70	55
	5	405	694	+2.79	7.7	+	+	Apr. 16	85	60
	3	437	945	+3.17	9.3	+	+	Apr. 14	70	80
Controls		392	601	+2.16	18.0	0	0			
		446	891	+2.79	18.9	0	0			
		409	667	+1.92	16.7	0	0			
		359	472	+2.19	18.4	0	0			

[1]Died; Stage III ova in ovaries.

pigmented at 1 day and the mouth was functional at 1-3 days after hatching. No abnormalities were observed in hormone-induced larvae.

Twenty larvae were sampled weekly (Table 4). The specific growth rates for the 63-day period from first feeding averaged 9.97%/day for dry weight (micrograms) and 2.75% standard length (millimeters). The first fish metamorphosed 54 days after hatching at 17.00 mm standard length. By the 63d day after hatching, all the larvae had completed metamorphosis, and average length was 17.40 mm.

Wild copepod nauplii were collected daily from a nearby estuary and fed to the larvae after being sieved to obtain the proper particle size. Larvae of the yellowtail flounder required small food organisms (<100μm in largest dimension) to initiate feeding. The most difficult aspect of rearing the larvae was the problem of obtaining enough food organisms in the size range required. Larval mortality was high for the first 2 wk of feeding, possibly caused by starvation. However, yellowtail flounder larvae are able to survive for considerable periods of days without exogenous food. Some larvae were maintained at 8°C and fed successfully and survived after being deprived of food for 10 days after hatching (Smigielski unpubl. data). As the larvae increased in size through metamorphosis, larger food organisms such as adult copepods, the rotifer *Branchionus plicatilis*, and the brine shrimp, *Artemia* sp., were offered.

TABLE 4.—Size of yellowtail flounder larvae reared artificially at 10°C from hac ing to metamorphosis. Average sizes of 20 larvae are followed by standard deviation.

Days after first feeding	Mean length (mm)	Mean dry weight (μg)
1	3.08±0.20	16.2±4.3
7	3.39±0.25	19.8±4.3
14	5.16±0.47	56.0±20.1
21	5.92±0.79	89.9±57.4
27	6.82±0.51	126.5±34.0
34	6.68±0.89	161.5±66.4
41	8.95±1.03	608.6±340.2
48	10.53±4.38	1,133.3±1,267.8
55	14.73±3.98	5,576.6±2,694.1
63	17.40±2.33	8,635.9±3,059.4

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TRACE METAL CONTAMINATION OF THE ROCK SCALLOP, *HINNITES GIGANTEUS*, NEAR A LARGE SOUTHERN CALIFORNIA MUNICIPAL OUTFALL[1]

Los Angeles County's submarine discharge of municipal wastewater from the Joint Water Pollution Control Plant (JWPCP) off Palos Verdes Peninsula is the single largest anthropogenic source of trace metals to the marine ecosystem off southern California. The 1974 annual mass emission rates of chromium, copper, and zinc via this discharge (4.8×10^{11} l/yr, which underwent primary treatment only) were about 400, 300, and 850 t, respectively; these were approximately 10 times the corresponding inputs measured in 1971-72 surface runoff from southern California (Young et al. 1973). As a result, bottom sediments around this submarine outfall system are highly contaminated by a number of trace metals (Galloway 1972; Young et al. 1975). Here we report abnormal levels of seven metals in three tissues of the filter-feeding rock scallop, *Hinnites giganteus*,[2] that was collected in the discharge zone and thus had been exposed to suspended wastewater particulates. (The adductor muscle of this bivalve mollusc is considered to be a delicacy, and scallops near the discharge are sought by sport divers.)

Procedures

During 1974, divers collected eight scallops within the size range generally consumed (10 to 25 cm in diameter) from depths of about 20 m at three stations in the discharge zone between Whites Point and Point Vicente: these stations were <1 km off Palos Verdes Peninsula. Six scallops in the same size range also were taken from control stations at similar depths off Santa Catalina and Santa Barbara Islands (Figure 1). To check our 1974 results, during 1976 eight specimens within this size range were again collected from this region in the discharge zone. However, we were not able to obtain additional island samples; therefore, five specimens were collected from each of two coastal stations located approximately 50 km to the north and south of Palos Verdes Peninsula. The samples were frozen in plastic bags after collection. Later, digestive gland, gonad, and adductor muscle tissues were excised from each specimen before it was fully thawed, using a new carbon steel scalpel and a cleaned Teflon[3] sheet; the tissues were placed in cleaned polyethylene vials. Care was taken to avoid contaminating the gonadal or muscle tissue samples with sediments or juices from the digestive glands.

Following dissection, each sample (1 to 2 g wet weight) was digested in 10 ml of a 1:1 nitric acid

[1]Contribution No. 85 of the Southern California Coastal Water Research Project.

[2]Formerly *Hinnites multirugosus* (Roth and Coan 1978).

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

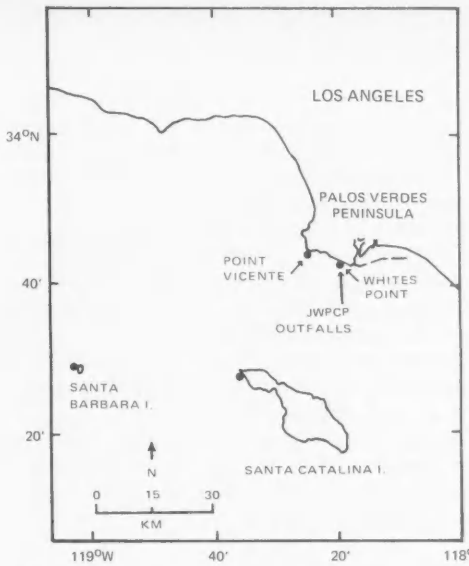

FIGURE 1.—Outfall and island control sites off Los Angeles, Calif., for collection of rock scallops.

solution (ultrahigh-purity reagent grade) until the remaining volume was about 3 ml. This procedure was repeated once, and the final residue was filtered through an acid-washed Whatman No. 40 filter. The filtrate was then diluted to an appropriate volume, and the treated sample was analyzed by atomic absorption spectrometry. Silver, chromium, copper, nickel, and lead were measured by injecting 2.5 μl of sample into a graphite furnace; cadmium and zinc levels were determined by aspirating the sample into an air-acetylene flame.

Process blanks were analyzed with all samples. Typical blank corrections were <10% of the gross concentrations observed, except for chromium, nickel, and zinc in adductor muscle, where the blank corrections were 15-20% of the gross concentrations. To test digestion efficiency, residues collected after filtration were redigested following the same procedure employed initially but using only 5 ml of 1:1 nitric acid solution; levels measured in the residue generally were <5% of the concentrations found in the first digestion. In addition, using this procedure on Standard Reference Material No. 1571 (orchard leaves) we have obtained values for our target metals which are within the ranges reported by the National Bureau of Standards (NBS); in all cases our results agreed within ±20% of the NBS values.

Results and Discussion

A comparison of the 1974 and 1976 results indicated that, for each of the seven metals studied, there were no significant differences between levels in the Palos Verdes scallops collected during the 2 yr. Therefore, the data from these 16 specimens have been combined to obtain an estimate of metal concentrations in scallops around the JWPCP submarine outfalls (Table 1). However, distinctly higher levels of silver, chromium, and copper were measured in the specimens from the other two coastal stations, compared with those in the scallops from the island control sites. Alexander and Young (1976) also observed elevated concentrations of these three metals in digestive glands of the intertidal mussel *Mytilus californianus* collected within 100 km of Los Angeles, indicating the widespread influence of municipal wastewater discharges on distributions of silver, chromium, and copper in the nearshore marine ecosystem of southern California. Therefore, we have used only the data from the six island specimens to estimate natural concentrations of the target trace metals in the three scallop tissues investigated (Table 1). For each metal we have calculated a "contamination factor," defined as the

TABLE 1.—Trace metal concentrations (mg/wet kg) in tissues of rock scallops collected during 1974-76 from the Palos Verdes outfall zone (16 specimens) and from island control stations (6 specimens). Single and double asterisks indicate experimental results are significantly different from control results at $P<0.05$ and $P<0.01$, respectively.[1]

	Digestive gland		Gonad		Adductor muscle	
Metal	Outfall	Control	Outfall	Control	Outfall	Control
Silver:						
Mean	2.0**	0.31	0.21**	0.018	0.016	0.010
±SE	0.34	0.068	0.071	0.008	0.004	0.003
Cadmium:						
Mean	430	550	5.0	5.5	0.92**	0.34
±SE	76	61	1.4	2.3	0.070	0.027
Chromium:						
Mean	42**	2.2	8.8**	0.39	0.33**	0.050
±SE	5.7	0.48	3.0	0.049	0.038	0.025
Copper:						
Mean	210**	65	3.7*	2.3	0.32*	0.16
±SE	25	16	0.52	0.49	0.058	0.042
Nickel:						
Mean	1.1	1.5	0.36	0.26	0.14	0.12
±SE	0.13	0.11	0.12	0.10	0.034	0.050
Lead:						
Mean	9.3	4.4	<0.08	<0.06	<0.05	<0.03
±SE	1.8	1.4	—	—	—	—
Zinc:						
Mean	120	100	38*	20	22	22
±SE	10	17	3.9	7.2	1.7	0.69

[1]Determined by the nonparametric 2-sided Mann-Whitney *U* Test.

ratio of the mean concentrations for the outfall and control samples (Table 2).

It seems clear from these data that rock scallops living inshore of the JWPCP discharge accumulate trace metals at above-normal levels. Application of the 2-sided Mann-Whitney *U* Test (Tate and Clelland 1957), a nonparametric test which assumes neither normality nor homogeneity of variance, indicated that, in 10 of the 19 comparisons, the experimental (JWPCP) results are significantly different from those of the controls (Table 1). In all 10 of these cases the experimental means are higher.

In our past studies with molluscan bioindicators, we have generally used digestive gland concentrations to locate possible metal contamination because concentrations are usually higher in this tissue than in the gonad or adductor muscle (Alexander and Young 1976; Eganhouse and Young 1976). However, these values may not be representative of the degree to which metals are actually incorporated into the body tissues because the digestive gland sample may contain ingested particulates contaminated by metals that are not biologically available. Therefore, the gonad and muscle contamination ratios found in this study are of special interest. In 7 of the 12 comparisons, the experimental results were found to be significantly higher than those of the controls (Table 2). For five of the six metals measurable (lead was undetectable in these tissues), at least one of the two contamination ratios is essentially ≥ 2. In addition, we found the mean concentration (± 1 SE) of total mercury in adductor muscle of three Palos Verdes scallops to be 0.059 ± 0.005 mg/wet kg. This value is more than twice the mean concentration measured in three island specimens (0.027 ± 0.008 mg/wet kg). However, it should be noted that mercury levels in the Palos Verdes specimens were still an order of magnitude below the U.S. Food and Drug Administration action level of 0.5 mg/wet kg in seafood intended for interstate commerce.

TABLE 2.—Contamination factors[1] for seven metals in three tissues of rock scallops from the Palos Verdes outfall zone and island control stations. Factors indicate experimental to control ratios for mean concentrations (Table 1).

Metal	Digestive gland	Gonad	Adductor muscle
Silver	6.5**	12**	1.6
Cadmium	0.78	0.91	2.7**
Chromium	19**	23**	6.6**
Copper	3.2**	1.6*	2.0*
Nickel	0.73	1.4	1.2
Lead	2.1	—	—
Zinc	1.2	1.9*	1.0

[1]Single and double asterisks indicate significant differences between experimental and control results at $P<0.05$ and $P<0.01$, respectively.

As shown in Table 1, the mean concentration of lead in the digestive gland of the outfall scallops was 9.3 mg/wet kg, approximately 100 and 200 times the upper limit concentrations measured in the gonadal and muscle tissues, respectively. These results indicate that elevated concentrations of other metals measured in the gonad and muscle tissues were not caused by contamination from the digestive gland during dissection. Thus, rock scallops exposed to municipal discharges do appear to be capable of physiologically incorporating at least six potentially toxic trace metals in their gonadal or muscle tissue to levels at least twice normal concentrations.

The mean values for cadmium in the digestive gland and gonads of the Palos Verdes specimens were somewhat lower than those for the island controls (Table 1); the respective outfall-to-control ratios were 0.80 and 0.92. We have made similar observations in previous studies of metals in flatfish taken by trawl from the two areas (de Goeij et al. 1974; McDermott, Alexander, Young, and Mearns 1976). Liver tissue from Dover sole, *Microstomus pacificus*, collected during 1971-72 and known by their high DDT levels and high incidence of fin erosion disease to have inhabited the highly contaminated sediments, were shown by neutron activation analysis to have significantly lower concentrations of cadmium than did the livers of island control specimens; the outfall-to-control ratio was 0.33 (de Goeij et al. 1974). Analyses of subsequent collections (1972-73) using a different laboratory and analytical technique (arc emission spectroscopy) confirmed this observation, yielding an outfall-to-control ratio of 0.59 (McDermott, Alexander, Young, and Mearns 1976). In addition, analyses by atomic absorption spectroscopy recently conducted in our laboratory revealed depressed cadmium concentrations in livers of diseased flatfish collected during 1976 and 1977 off Palos Verdes Peninsula and in Seattle's Duwamish River Estuary (two regions highly contaminated by chlorinated hydrocarbons); relative to control levels, the corresponding concentration ratios were 0.60 and 0.30, respectively.[4] Further, analyses of digestive glands of intertidal mussels we collected at the base of the

[4]Sherwood, M. J. 1977. Fin erosion disease and liver chemistry: Los Angeles and Seattle. *In* Coastal water research project annual report, p. 213-219. South. Calif. Coastal Water Res. Proj., El Segundo. NTIS PB274463/AS.

Palos Verdes outfalls and at island control stations during 1971 yielded[5] an outfall-to-control ratio for cadmium of 0.81.

The relatively low cadmium levels often found in some tissues or organisms living around the Palos Verdes outfalls may be related to the high levels of chlorinated hydrocarbons that have accumulated there from past wastewater discharges. Concentrations of total DDT and total PCB in mussels, sediments, and flatfish from the region are 100 to 1,000 times those measured in samples from island control areas (Young et al. 1976: McDermott, Young, and Heesen 1976). Recently, Nimmo and Bahner (1976) reported that exposure of a penaeid shrimp to methoxychlor (a chlorinated pesticide somewhat similar to DDT and PCB) appeared to depress concentrations of cadmium in this organism. It is possible that animals off Palos Verdes are showing a similar effect.

Conclusions

The data presented here indicate that the submarine injection of primary-treated municipal wastewater can lead to distinct trace metal contamination of filter-feeding rock scallops within a few kilometers of the discharge. Mean values for silver, cadmium, chromium, copper, mercury, and zinc in gonadal and/or muscle tissue of specimens collected near the Los Angeles County outfalls ranged from approximately 2 to 23 times the corresponding means for control specimens. These elevations do not appear to be artifacts caused by contamination from particulates in the digestive gland, but rather to result from actual physiological uptake of the metals. Although the results of this study point to a potential problem from waste metals discharged via municipal outfalls, we do not yet know the degree to which such elevated metals affect the rock scallop or its predators.

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[5]Southern California Coastal Water Research Project. 1973. The ecology of the Southern California Bight: Implications for water quality management. South. Calif. Coastal Water Res. Proj., El Segundo, TR 104, 531 p. NTIS PB274462/AS.

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